STUDIES IN THE INHERITANCE OF DISEASE-RESISTANCE.

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In a previous paper dealing with the inheritance of certain characteristics of wheat, evidence was brought forward to show that it was probable that liability and immunity to the attacks of yellow rust (*Puccinia glumarum*), were a pair of characters in the Mendelian sense of the word[1]. The evidence was as follows: Rivet wheat, a variety which is only slightly attacked by this parasite, was crossed with an extremely susceptible variety Red King. The latter is a hybrid descended from Michigan Bronze, which in turn is extremely susceptible to yellow rust. The resulting hybrids were as susceptible to the attacks of yellow rust as the parent Red King, whilst the generation raised from them consisted of individuals which were either slightly or excessively susceptible to the disease. There was a general agreement between the extent of the disease in these two classes and in the two parents, and further the proportions of badly to slightly attacked were in the ratio of 3 : 1. In the following generation the relatively immune individuals bred true to this character, though not necessarily to other characters as well, but the susceptible types taken as a class produced either all susceptible offspring or a mixture of susceptible and relatively immune—the result expected if these characters are Mendelian. Unfortunately the statistics for this last generation were not altogether satisfactory, partly owing to unfavourable conditions at the sowing time and partly owing to the excessive mortality of the diseased individuals in the preceding generation which limited the amount of grain harvested for this trial.

While the experiments were in progress a further series was commenced in order to obtain data on a more extensive scale and

[1] Biffen, *Journ. Agric. Sci.* Vol. I. p. 40.

also to determine whether immunity to the attacks of other fungi could be traced in a similar fashion.

A survey of the commoner plant diseases seemed to indicate that the Uredineae were the most suitable for this purpose and that the yellow rust offered unusual advantages, owing to the fact that one could count with no small degree of certainty on there being sufficient rust each season to thoroughly expose all plants to the chance of infection without having recourse to artificial inoculation. In this district a year never passes without there being a more or less severe epidemic of yellow rust, so that under ordinary circumstances there appeared to be no likelihood of failure through lack of suitable external conditions.

The black rust (*Puccinia graminis*) was also included in these experiments, though it was not expected to be so satisfactory for an investigation of this kind, owing to the fact that its appearance on the plots at the University Farm is generally late in the season. It rarely occurs before the middle of June and by that time the foliage of the wheat is often partly killed by the attacks of yellow rust. In some seasons no signs of it are to be met with. On the other hand the importance of the disease from an economic point of view had to be considered, and as a plentiful supply of infecting material could generally be obtained from its alternate host plant, the barberry, growing in a neighbouring hedgerow it was resolved to make the attempt and resort to artificial infection should the natural fail.

The investigation of the inheritance of liability to the attacks of a totally different group of fungi seemed essential, and as it was desired to work as far as possible with cereals the mildew *Erysiphe graminis* was chosen. Experiments with the biologic forms on both wheat and barley were planned but in the end only that on barley was carried to its conclusion.

The chief points of the life history of these parasites as far as they are concerned in this investigation may be briefly stated here[1].

The presence of *Puccinia glumarum* is indicated by the formation of numerous shortly elliptical pustules which break through the epidermis of the host plant—in this case wheat—and shed masses of spores known as uredospores. In the mass these have a characteristic deep cadmium yellow colour. These spores if applied to the surface of a variety of wheat susceptible of infection germinate and push hyphae

[1] For a complete account and figures, reference may be made to Eriksson, *Die Getreideroste*, p. 141.

through the stomata, the mycelium then penetrates the intercellular spaces and drives haustoria through the walls of adjacent cells in order to obtain nutriment. If the conditions are favourable for development the mycelium will produce a fresh crop of uredospores in about ten days. Under these circumstances the spread of the disease is often exceedingly rapid and it is no unusual occurrence to see a field which is apparently rust free coloured yellow with the rust a week later. The period at which the uredospores are first noticed here is very variable, ranging from the beginning of March until the middle of May. Their formation continues until the foliage begins to die, generally about the middle or end of July, and then the mycelium produces a second spore form, the teleutospore, in small, flat sori. Whether a third spore form, the aecidiospore, is produced, as is the case with so many other Uredineae, is open to question, and the view is gaining ground that the fungus is homoecious.

The black rust (*Puccinia graminis*) forms darker masses of uredospores in longer sori and the teleutospores are produced in characteristic linear pustules surrounded by the torn edges of the epidermis of the host. As is well known an aecidial stage occurs on the barberry. The infection of wheat is readily brought about by uredospores or by aecidiospores, either of which produce crops of uredospores. The details of infection are very similar to those of the yellow rust.

The biologic form of *Erysiphe graminis* on barley forms a web or felt-like coating on the stems and foliage which at the period of spore formation becomes pulverulent. The fungus is distributed throughout the summer by conidia which on germination give rise to an epiphytic mycelium attached to the plant by haustoria driven into the epidermal cells. No deep-seated mycelium similar to that of the rusts is produced.

A considerable collection of both wheats and barleys was obtained and in order to select the most suitable varieties for this investigation the incidence of these three parasites was observed in detail during the year 1902. A similar series of observations had previously been made in Sweden by Eriksson[1], but in view of the fact that it is often stated that susceptibility to disease varies with climatic conditions it was thought necessary to cultivate and test the varieties under the conditions which would obtain during the experiments. In Eriksson's trials the varieties are grouped into five classes ranging from 0 with no disease to 4, very badly diseased. The attempt was made to classify

[1] Eriksson, *ibid.* pp. 333 and 342.

the series in a similar way. In all cases where Eriksson placed a variety in either of the extreme classes the results were the same on my plots, but there was often a difficulty to decide between classes 2 and 3 and 3 and 4. Where no actual standards for comparison were available this was only to be expected and the general impression which remained was that Eriksson's classification agreed well with the one made under the conditions obtaining on the Cambridge plots.

From amongst the series representatives of each class were selected and these have been kept under cultivation since, the remainder, except a few required for other experiments, being discarded. Since 1902 the rust epidemic has varied considerably in its intensity, but the varieties have still retained their relative positions on the arbitrary rust scale with one possible exception. This was a variety known as New Era which originally was placed in class 1, *i.e.* slightly susceptible. In 1906, a year in which there was comparatively little rust, it remained practically rust free until the foliage was beginning to die, when pustules appeared.

The immune varieties chosen were Einkorn, Hungarian Red and "American Club." Each of these has been kept under continuous observation, and in order that there should be no question of their not being exposed to infection they have been grown in company with the susceptible forms whose rust-coated leaves have continually overlapped them. In addition, once or twice each season they have been watered overhead with a fine spray containing quantities of uredospores in suspension.

Einkorn (*Triticum monococcum vulgare*, Kcke). This variety tillers to an enormous extent, forming a thick turf of foliage. It is notoriously rust-resistant though this dense mass of foliage would seem to provide excellent opportunities for infection. In Eriksson's trials it was the only variety immune to the three common wheat rusts. Reports from various parts of the world show that this characteristic is retained under various climatic conditions. On the Cambridge University Farm the variety has been entirely rust free each season with the exception of 1906 when on some fifty plants two leaves were found late in the season on which a few scattered pustules occurred. The majority of these were unbroken and shed no spores before the death of the leaves.

Hungarian Red. The grain of this variety was obtained under the name of "Ungarischer roter" from Haage and Schmidt of Erfurt. It is probably identical with the variety examined by Eriksson. In his

trials it proved immune to *P. glumarum*, but not to *P. dispersa*, except in the rust year 1892 when it was slightly attacked. In the trials at Cambridge it has been perfectly free from the yellow rust but no statements can be made as to its susceptibility to the attacks of other species, for their appearance during the last four seasons has been too spasmodic to ensure fair tests. It has proved a feebly growing variety and its development is often crippled by attacks of *Erysiphe graminis*.

"American Club." This is a variety of *Triticum compactum* which so far I have been unable to identify with certainty. Its morphological characters agree with those of Bearded Herisson or Hedgehog wheat, but whereas this is susceptible to yellow rust the American Club is immune. It was obtained from Mr A. E. Humphries, who found it growing in a plot raised from a commercial sample of Northern Duluth wheat. This, as usual, was graded wheat and among numerous other varieties contained a small proportion of the variety in question. By chance my culture was sown between plots of Michigan Bronze and Hungarian White, another highly susceptible wheat. Throughout the late spring and summer of 1904 its plot was a vivid green colour contrasting markedly with the bright orange yellow of its neighbours which were so badly infected that the soil below them was tinged with the masses of uredospores produced. Late in the season the plants were covered with aphis and the coating of honeydew provided a substratum for the growth of *Cladosporium herbarum*. Yet though the plants were continually exposed to infection and in the latter part of their development under peculiarly unfavourable conditions for healthy growth they remained entirely free from yellow rust.

Since then some three hundred plants have been grown and kept under close observation and only two immature pustules have been found. These occurred in August 1906 on leaves again covered by aphis. The pustules did not break through the epidermis and it is impossible to be certain, though on the whole it is probable, that they were yellow rust. In colour they were slightly darker than normal yellow rust, but their almost circular shape would distinguish them from the more linear pustules of black rust.

It is probable that this variety is susceptible to both black and brown rusts but so far the evidence to hand is not complete[1].

[1] Since writing the above, reports from the Transvaal and from Canada, where small sowings of this variety have been made, show that it is very susceptible to the black rust. It is possible that this is the wheat known as Kidd in Canada, which is similar morphologically and known to be susceptible to this rust.

In describing these varieties as immune it is essential that attention should be called to the fact that they are immune under the ordinary conditions of cultivation of wheat. Absolute immunity under all conditions is not to be expected in any wheat where the rusts are in question. In fact it is practically impossible to say that any plant is immune to the attacks of wheat-rusts if the preliminary stages of infection are to be taken as evidence of susceptibility, for the uredospores germinate on the majority of phanerogamous plants and push hyphae through the stomata into the intercellular spaces[1]. Under such circumstances no further development occurs and the mycelium perishes.

Further emphasis has to be laid on the importance of natural conditions for the development of the host plant, since Salmon[2] has shown that barley foliage may be infected with the biologic form of *Erysiphe graminis* found on wheat if only it is exposed to sufficiently drastic conditions. To secure infection the leaves have to be chloroformed, scorched, bruised, etc. and when their vitality is sufficiently lowered the mildew from the wheat succeeds in getting a hold and developing sufficiently to produce a feeble crop of conidia. Yet under normal conditions infection is impossible. As a matter of fact in the three varieties selected for these experiments the early stages of infection are readily observable in preparations made from foliage growing in the open, but the growth of the mycelium is quickly inhibited and it dies without causing any noteworthy injury to the host. As will be shown later there is also the possibility that infection may occur on foliage which is passing over to a moribund condition. Details of the histology of infection are published by Miss Marryat in this number of the Journal.

Of the slightly susceptible varieties which have been crossed with immune types the more important are Street's Imperial (Class 2) and New Era (Class 1). These grown under the same conditions as the immune varieties have each season produced numbers of sparsely scattered pustules on all of their leaves. In 1906, a poor rust year, the infection was less marked than usual and only occurred late in the season. Of the two, Street's Imperial is the more susceptible and it may be taken to represent roughly the extent to which the majority of our English varieties are susceptible. The varieties characterised by

[1] De Bary, *Comp. Morph. and Biology of the Fungi*, p. 361. Gibson, *New Phytologist*, Vol. III. p. 184.

[2] Salmon, *Anns. Bot.* Vol. XIX. p. 125.

excessive liability to infection which have been used as parents are "American 1," "American 2," Preston, Hungarian White, "Tasmanian" and Michigan Bronze. These are placed as far as possible in the order of their susceptibility.

"American 1 and 2" are varieties grown from graded Northern Duluth and Manitoba wheat. Both are varieties of *Triticum vulgare* but their local names are unknown to me. The following short description may aid in their recognition in Canada and the United States where they are probably commonly cultivated. Number 1 has lax, beardless ears with a yellow chaff: number 2 a similarly shaped ear with white chaff.

Preston is a Canadian wheat of hybrid origin.

Hungarian White, a variety from Haage and Schmidt. This Eriksson puts into classes 4 and 3, stating that it is very susceptible to yellow rust in Sweden. Each of these four varieties throughout the seasons 1903—6 inclusive has been badly attacked and it would have been difficult to count the pustules on any of the diseased leaves. In each case though the plants set a fair quantity of grain.

"Tasmanian" (a variety sent from Tasmania: proper name unknown to me) is very similar to Rough Chaff as far as external appearances go but distinguished from it by extreme liability to the attacks of yellow rust. There is little to choose between this and the succeeding variety in this respect.

Michigan Bronze has earned the reputation of being one of the most susceptible varieties in existence, and on this account it has been largely used by Eriksson in his researches[1]. The pustules generally appear on this wheat earlier than on other varieties and they quickly become so numerous that the whole of the foliage appears to be coated with rust. Every part of the plant is attacked and whereas the upper leaves, chaff and awns of moderately susceptible varieties rarely carry many pustules, in the case of Michigan Bronze these structures are as badly infected as the lower leaves. So severe is the attack that the plants set little or no grain on my plots. In 1906 for instance a plot of forty plants did not produce a single grain. Owing to this difficulty of obtaining seed the stock has to be renewed from year to year and in consequence the plants used for comparison with the hybrids are not, as one would prefer, the direct descendants of the one used as pollen plant. The stock of "Tasmanian" has died out altogether.

[1] Eriksson, *Ann. d. Sc. Nat.* T. xiv. p. 107, 1901.

Some eight hundred plants of these two varieties have been grown since 1902 and not one has escaped infection. So certain is the incidence of the disease that a practice has been made of planting rows of Michigan Bronze among the hybrids in order to ensure the presence of numerous centres of infection. During this last season this precaution was abandoned as unnecessary.

In making the crosses between immune and excessively susceptible varieties the immune parent was in each case the mother plant. Reciprocal crosses were not attempted, since previous experience had shown that there was little likelihood of their succeeding. Where moderately susceptible varieties were under experiment such crosses were successfully attempted.

The following crosses were made between excessively susceptible and immune types:

1. American Club × American 1.
2. „ „ × American 2.
3. „ „ × Preston.
4. „ „ × Tasmanian.
5. „ „ × Michigan Bronze.
6. Hungarian Red × Hungarian White.

The hybridising was carried out in 1904 and the resulting plants were kept under observation throughout the period of their growth in 1904—5. Yellow rust was first observed in the neighbourhood on March 3rd. By May 11th the attack seemed fairly general and wheat in the same field as the hybrids was showing signs of a bad rust season approaching. At this date the hybrids were standing about six inches high. The condition of the plants then was:

1. One plant only: the three lowest leaves badly attacked, the upper leaf still free from rust. This plant was killed shortly after by wireworm.

2. Three plants: a few broken pustules on the lowest leaves, foliage becoming brown and showing numerous dead areas (probably not due to rust).

3. Rust pustules numerous on all the leaves, plant very vigorous.

4. Three plants: all very badly infected with fewer pustules on the highest leaves.

5. Nine plants: the extent of infection differed on individual plants:

(*a*) leaves as far as the fourth one badly infected.
(*b*) leaves as far as the second one badly infected.
(*c*) leaves as far as the fourth one badly infected.
(*d*) leaves as far as the fourth one badly infected.
(*e*) rust on first and second leaves only.
(*f*) on the three lower leaves, upper quite free.
(*g*) infected badly as far as the fourth leaf.
(*h*) almost rust free: only a few scattered pustules on the lower leaves.
(*j*) three lower leaves infected, upper free.

All of these plants were particularly vigorous. Those most badly infected appeared to be diseased to the same extent as Michigan Bronze.

6. Six plants: five of these were uniformly infected up to the fourth leaf, one was entirely rust free. This last plant proved to be a pure Hungarian Red in the next generation, the result of accidental self-fertilization. During June the rust spread rapidly, causing an epidemic of over-average severity. By June 22nd the condition of the plants was as follows:

2. Every leaf dead and covered with the remains of pustules. Death was probably due to other causes besides the rust.
3. Foliage still living and densely coated with pustules.
4. Lower leaves dead, the upper with innumerable pustules.
5. All parts of the plants thickly coated with rust.
6. Very badly infected.

The ears were pushed through the sheaths a week later and the flowering stage was passed. In each of the five series including number 2 the glumes and paleae were becoming infected and pustules had already broken on the awns of the hybrid American Club and Michigan Bronze. At this stage the general appearance of the plants with regard to the amount of rust upon them was very similar to that of the susceptible parents and it was problematical whether enough grain would be secured to carry the experiment on to the next generation. At harvest, however, 4, 5 and 6 yielded a fair crop, far more in fact than the susceptible parents. This may point to the fact that the hybrids were not as badly attacked as the latter and that they were intermediate in this respect, or a possible explanation is that the vigorous growth so characteristic of the F. 1 had enabled the plants to withstand the attack better than the susceptible parents.

Most of the grain harvested was, as was only to be expected, badly

shrivelled but its germinating capacity was fairly satisfactory. It was sown early in the autumn of 1905 under normal conditions of cultivation, part on land which had previously carried a wheat crop, part on soil which was in better condition as it had just previously carried a clover crop. The varying soil conditions made no difference in the final results. The grain from each ear of each plant was sown separately in the case of numbers 5 and 6.

No yellow rust was found on the plots until May 16th, an unusually late date for this district. It occurred on some plots not included in this experiment, but the following day unmistakable signs of rust were found on the series with Michigan Bronze as the parent. By the 29th of this month infection appeared to be fairly general on all the plots. At this date the plants were standing about two feet high and they were in a thoroughly vigorous condition. By June 11th it was judged that any plants susceptible to the disease would have had sufficient opportunity for infection as the plots were fast assuming a bright orange colour and an examination of each individual was commenced.

American Club × Michigan Bronze. Every leaf on the plants, the dead and dying basal leaves included, was carefully inspected and wherever the slightest signs of infection could be detected the plant was entered up in the note-book as susceptible. All diseased plants were cut back to within one foot of the ground whilst the immune plants were left standing to give them further opportunities for infection. The detailed figures for the descendants of plant 5 *a* may be quoted to show the incidence of the disease at this date:

Ear	Rust free	Susceptible
1	9	21
2	9	24
3	9	26
4	8	13
5	17	41
6	7	19
	59	144

Plants 5 *b*, *c*, *d*, and *e* were examined in the same way between the 11th and the 18th of June, the susceptible plants being again cut back. The statistics were as follows:

b	57	141
c	61	128
d	43	147
e	51	157
Total, including 5 *a*	271	717

The plants left standing on these plots were examined at intervals between July 6th and the 16th and a small number of rust susceptible plants were found:

	Rusted	Revised totals Free	Rusted
in 5 *a*	3	56	147
5 *b*	12	45	153
5 *c*	14	47	142
5 *d*	7	36	154
5 *e*	7	44	164
	Total	228	760

In the meanwhile the foliage of the remaining plots of this series was turning yellow and dying off and teleutospores were being formed. As there appeared to be no possibility of susceptible plants having escaped infection at this date the plants were pulled up by the roots in order to make the examination more rapidly, some fifty infected ones being left for seed. Plants 5 *f*, *g*, *h* and *j* gave a total offspring of 1244, 295 of which were free from yellow rust and 949 badly infected. The whole series thus yielded 523 immune and 1609 susceptible individuals.

The immune plants which had been left standing remained green longer than the diseased ones, and their foliage did not commence to turn colour until July 24th. The leaves remained flat and polished and the straw was either a vivid red or yellow colour very unlike that of the neighbouring plots, which, as is the case with most wheats, turned a dull brown owing to the attacks of *Cladosporium herbarum* following the rust. The immune plants could readily have been sorted by the brilliancy of their colour alone.

Whilst the foliage was dying during the last week of July the immune plants were again examined in detail. They were now surrounded by strongly growing branches thrown up by the plants previously cut back and these were carrying an unusually heavy crop of uredospores. The plants were thus exposed to infection at a time when as a rule no uredospores are being formed on wheat. In addition to yellow rust these new branches were infected with both black and brown rust. Symptoms of infection were found on at least twenty of the immune plants; the symptoms being either discoloured areas on the bright yellow ground or in some cases distinct pustules. In all cases these pustules were small and unbroken and they had shed no uredospores when the leaf shrivelled. It is impossible to say whether

these immature pustules were those of *P. glumarum* or one of the other cereal rusts. On the whole I am inclined to think that they belong to the former species, and that when the chlorophyll contents were broken down, foodstuffs translocated for the finishing grain and the vitality of the leaf exhausted it became a prey to the fungus[1]. Assuming these immature pustules were those of the yellow rust this is not an unreasonable explanation though it is a little strange that no pustules could be found on the dying basal leaves earlier in the season. These twenty plants have not been included in the total of rust-susceptible plants.

In addition to the series described, about a hundred plants of the same parentage have been used for infection experiments and for pot cultures for demonstration at the Derby Show of the Royal Agricultural Society and at the Conference of Plant Breeders at the Royal Horticultural Society. No statistics of the number of immune and susceptible plants have been kept in these cases.

Concurrently with this segregation into immune and susceptible forms there was of course the usual segregation of other Mendelian characters. The two parents do not show many pairs of differentiating characteristics, the most important pair being lax and dense ears. There are slight foliage differences but these are not marked enough to discriminate with any certainty. The hybrid plant had dense ears which at first sight were very similar to those of the American Club, but which on measurement were found to be intermediate between lax and dense. The whole habit of the plant, excluding its susceptibility to yellow rust, was very similar to that of the mother parent. In the following generation lax, intermediate and dense eared individuals, occurred in, as a small trial count showed, the usual ratio of 1 : 2 : 1[2]. The immunity and susceptibility were distributed impartially over each of these groups. The plants with lax ears were similar to Michigan Bronze, and those with dense ears to American Club, so that immune types of Michigan Bronze and susceptible types of American Club have been bred. In other words the factors which determine immunity or the reverse are transmitted as Mendelian characters.

Whether this is due to the presence of toxins and antitoxins, as seems probable, further research will have to decide.

[1] It is a well known fact that fungi can readily attack withering or even resting plant tissues which in a normal or an active state are immune. Hartig for example has shown that the mycelium of *Peziza Wilkomii* can only work its way through the tissues of the larch when in a resting condition.

[2] Spillman, see *Journ. Hort. Soc.* Vol. XXVII. p. 876.

From the statistics already quoted it is clear that if all plants which have become infected are grouped as susceptible, and those which have not as immune, then immunity is recessive to susceptibility, for they occur in the ratio of 1 : 3·07, a sufficiently near approximation to the ratio of 1 : 3. If this is the case, then, in the succeeding generation all the immune types will breed true to this character, while the susceptible types will breed true in the proportion of one in three. This part of the subject has still to be tested in this particular series, but in this connexion it may be noted that in a previous experiment the extracted (practically) immunes bred true to this character whilst the dominants split in some cases and bred true in others[1].

During the sorting of the plants into the two groups, however, another possibility presented itself. The extent of infection was obviously very different on different individuals. Whilst some were as badly diseased as Michigan Bronze others were, though by no means free from disease, relatively slightly infected. These latter plants produced considerably more grain than the very susceptible forms.

Thus fifty ears of the lax type taken at random produced 0·8 grms. where the plants were excessively susceptible, 64 grms. when moderately susceptible, and 145 grms. when immune.

These facts seem to point to the existence of intermediate liability in the heterozygote, for without question the less susceptible types were in the majority. The method adopted of cutting out each plant showing infection was not satisfactory for obtaining statistics of this sort, since intermediates would be grouped with extremely susceptible plants. If these indications are correct, and next season's tests will settle the matter, then instead of dealing with ordinary dominance the existence of intermediates will have to be recognised in the probable proportion of one immune and two intermediates to each extremely susceptible type.

Hungarian Red × Hungarian White (6)[2]. The F. 2 again consisted of extremely susceptible and immune individuals. A detailed examination of the series was not made until the third week in July, when the foliage was beginning to show symptoms of dying off. Twenty-four plants were entirely free from yellow rust and the remaining 109 were attacked to about the same extent as the susceptible parent.

American Club × American 1 (1). The grain from the F. 1 plants

[1] Biffen, *Journ. Agric. Sci.* Vol. I. p. 43.

[2] The statistics for this series were obtained by Mr S. V. Shevade of the Pusa Research Station, India.

did not in this case germinate satisfactorily, a sowing of about 250 only giving 83 plants. The majority of these were excessively rusted and many succumbed to the attacks of the parasite. Counted in the third week of July, 15 were completely rust free, 4 bore incipient rust flecks, and 64 were as badly attacked as the parent American 1.

American Club × Tasmanian (4)[1]. In the F. 2 series there was from the first a considerable difference between the extent of infection on the different susceptible plants and the attempt was made to grade them into immune, moderately susceptible and excessively susceptible forms. The first examination was made on June 19th. The number of diseased and disease free plants was then approximately equal, there being 39 of the former, and 37 of the latter. Of the 39 rusty individuals, 21 were moderately and 18 extremely susceptible. In the former group the pustules only occurred on the lower leaves whilst in the latter all the leaves were attacked. A second examination made on July 10th, showed no readily recognisable difference between the moderately and extremely susceptible individuals, though it is possible that if the count had been made before the heavy rains of the preceding week, which had washed the pustules clean, the two classes could have been distinguished. The final count gave a total of 56 rusty and 18 completely immune plants (two plants missed).

In the above cases one of the parents has been chosen for its excessive susceptibility to the attacks of yellow rust, whilst in those to follow slightly and moderately susceptible parents have been used in conjunction with an immune one. These less susceptible varieties were New Era and Street's Imperial. The former would, I think, be placed in Eriksson's class 1, the latter in class 2. In 1906, New Era was almost entirely free from rust until the end of the season, whilst Street's Imperial was only slightly attacked. Both varieties were crossed with American Club, and the F. 1's raised in 1905 matched the susceptible parent in the extent to which they became attacked.

The first generation from the hybrids of American Club and New Era remained almost rust free, and no attempts were made to obtain any statistics as to the incidence of the disease on the plots until the middle of July. A trial count then showed that the infected plants were roughly equal in number to the immune ones, and the further examination was delayed until the end of the month when the foliage

[1] S. V. S.

was showing symptoms of dying. The infected plants at this date showed few pustules on their foliage and none on the glumes and awns. Many had unbroken pustules and pale yellow flecks which possibly indicated abortive attempts at infection. All plants showing pustules were counted as diseased, with the result that 135 were placed in this class and 100 in the completely immune class. The plot contained about six hundred plants, but it was not thought worth while to examine the whole series. A comparison with the New Era at this period showed that the infection was unusually slight, and several of the plants only showed yellow flecks and no pustules. For some reason, probably connected with climatic conditions, the intensity of the attack was far less than it had been in previous years. This tendency to remain free from infection appears to have been retained in the F. 2 generation.

In the case of the hybrids with Street's Imperial and American Club, infection occurred early in the season, and there was from the first an obvious difference between the immune and susceptible individuals. When examined in detail on July 18th, 62 diseased plants and 22 immune plants were found on the plot.

One cross between two varieties, both susceptible to infection but differing in the intensity of the attack, has been kept under observation. The parents in this case were Rivet wheat and Emmer or *Triticum dicoccum*. The Rivet parent has for the last five years been slightly susceptible, and the rust has always been late in appearing on it. The Emmer is classed by Eriksson in group 2 in two seasons and group 3 in a third. No details with regard to its rustiness have been kept as the cross was originally intended for a study of the grain characters only. From the general agreement between my observations and Eriksson's with regard to the extent of the disease, it may be assumed that the rustiness of this variety would be the same in Cambridge as in Sweden. The F. 1 grown in 1905 was moderately susceptible to disease, and part of the F. 2 generation on June 20th consisted of 58 immune plants and 68 susceptible. On July 7th the whole plot was examined with the result that 204 plants were classed as rusty, 48 with traces of rust, and 23 immune. Tags were affixed to the immune plants in order to harvest them separately, as it was considered at this date that as they had resisted infection so long, they were probably really immune. The plants retained the green of their foliage longer than most of the hybrids (a characteristic of both parents) and during the first week in August it was found that those previously

marked as immune had become infected and bore pustules which had broken the epidermis. The totals thus became 204 moderately, and 71 slightly infected. The Rivet wheat was then examined and pustules were found on each of the 20 plants grown as a control, though the plants were free at the time at which the second examination of the hybrid plot had been made. Here as in the case of New Era and American Club the period at which infection occurs appears to be inherited as well as the susceptibility itself.

In addition to the series of F. 2 experiments already described, further generations of other crosses showing differences in the susceptibility of their parents have been kept under observation. In one case only was the cross made for this particular purpose, namely that between Red King and Rivet wheat already referred to. The extracted recessives only have been grown, and in the F. 4 they have retained their characteristic rust-resisting capacity unimpaired. The plots could be matched against the parent Rivet satisfactorily in this respect.

In a second case an extensive trial of a number of fixed types resulting from crosses between a susceptible Manitoban wheat and the far less susceptible varieties Rough Chaff and Lammas was being made for other purposes. Each of the plots of some forty of these fixed types contained some thousands of individual plants. Early in June symptoms of the coming rust epidemic were observable, and by the end of the month many of the plots were badly attacked, whilst their neighbours of the same descent, growing under identical conditions, were relatively free from disease. Two typical plots were examined in detail: in the first case every plant was found to be badly attacked, and the extent of the disease corresponded accurately with that of the Manitoban parent growing in a plot near, whilst in the other all the plants were slightly infected only. The extent of the disease probably corresponded with that of the relatively immune parent, though this could not be satisfactorily observed as no plot of this was grown under the same conditions. These plots represented all the possible combinations of the morphological characteristics of the parent varieties, and they afforded a striking field demonstration of the fact that there is no correlation between such characters and liability to the attacks of the yellow rust.

This was further illustrated in the case of a cross between Polish and Rivet wheat. The former has proved slightly more susceptible to the attacks of yellow rust than the latter, though the difference is by

no means as pronounced as in the case last described. A number of fixed types in the F. 3 generation were being tested for other purposes in 1905, and examples were repeatedly met with in which types as far as could be determined, absolutely identical with one another morphologically, differed markedly in rust resistance. Trial sowings in the following season showed that this peculiarity was retained.

Without doubt numerous other similar cases could have been found if all the hybrids then being cultivated could have been examined for these characters. Unfortunately in many cases no notes had been made as to the susceptibility of the parents, and the F. 1 and F. 2 generations had not been kept under special observation.

The attempt to determine whether the inheritance of immunity to the attacks of *Erysiphe graminis* was similar to that of yellow rust was made with both wheat and barley. The case of barley only will be considered here as the F. 2 generation of the wheat hybrid failed to become infected. The parent barleys were *Hordeum spontaneum* (Koch) and *Hordeum hexasticofurcatum* (K. H.). The former is as a rule completely free from mildew, whilst the latter is the most susceptible variety which could be found in a collection containing some 140 varieties. The crosses were, as in the case of most of the wheats, made on the immune parent. The resulting hybrid was attacked by the mildew, to, as far as one can judge such matters, the same extent as the susceptible parent. Its grains were sown in the spring of 1905 and gave a plot containing 79 plants. The Erysiphe did not appear until late in the season, though it was fairly abundant on field plots in the neighbourhood at an early date. The late infection may possibly have been due to the fact that the plants were unusually vigorous owing to their having been planted in garden soil at wide intervals. Fearing failure through lack of opportunity for continuous exposure to infection, artificial inoculation was resorted to. Leaves covered with mildew from a number of varieties were shaken up in water and the whole plot sprayed with it and then shaded for two days. This had the desired result, and a week later the whole plot was thick with mildew. On July 12th a detailed examination of the plot was made. The majority of the plants were very badly attacked, some bore traces of mildew, and a few were altogether immune. Those with traces of mildew and the immune individuals were kept under observation until the plants were beginning to show signs of the foliage drying preliminary to ripening, and at this stage the three types were sorted

out and counted. Fifty-six were badly attacked, 16 bore traces of mildew, and seven were altogether free from it.

At this time the parent *Hordeum spontaneum* was very slightly attacked, though no signs of disease had been seen in the two previous seasons, the severity of the attack corresponding with the traces of mildew found on some of the hybrids. The second parent *H. hexastico-furcatum* was badly diseased and matched the majority of the hybrids in this respect. No further generation of this cross has yet been grown.

The experiments with *Puccinia graminis* have not been altogether successful. The first attempts were made with Rivet wheat and Einkorn, the latter being used as the male parent in order to simplify the operation of crossing. Three strong F. 1 plants were raised in 1904, and as no black rust had appeared on these at the end of June, the plants were inoculated with aecidiospores from the barberry. Ten days after each plant was showing pustules which increased enormously in numbers, and by the time of harvest the straw was blackened with the gaping teleutospore sori. A few shrivelled grains were produced but these all failed to germinate, and in consequence no F. 2 generation was raised. The extreme susceptibility of the hybrid is rather unexpected, for Rivet wheat has not up to the present proved itself unusually so. A second F. 1 generation of this same cross has been raised, and this has entirely escaped infection with black rust, though slightly attacked with the yellow rust.

From analogy with the cases already described and from the susceptibility of the F. 1, it would appear that the susceptibility to black rust is also a dominant character.

From the foregoing series of experiments it is evident that the inheritance of immunity and susceptibility to the attacks of certain parasitic fungi can be traced as readily as that of morphological characters, and that immunity is recessive to susceptibility. Whether this is generally true or applies only to these special cases still has to be determined, but, for the time being, the fact that disease-resistance is recessive may be employed in attempts to cope with the losses due to the attacks of rust in cereals. Wherever these crops are cultivated the rusts take their toll, causing in the aggregate enormous losses. Thus in the rust year, 1891, Prussia alone is stated to have lost some £20,600,000, or approximately two-thirds of the value of the entire cereal crop[1], and according to M'Alpine[2], "at a

[1] *Zeits. für Pflanzenkrankheiten*, 1893, p. 185.

[2] M'Alpine, *Victorian Naturalist*, Vol. XXIII. p. 45.

low estimate it is considered that £100,000,000 does not cover the annual loss (due to rusts) to cultivated cereals alone."

The outcome of the numerous attempts made to minimize these losses is that prophylactic measures are useless, and the one hope left is to grow in each country varieties which prove rust-resistant. It has been known from comparatively early times that some varieties are more resistant than others. Thus Jethro Tull points out that "white cone or bearded wheat...is less subject to blight than Lammas wheat, which ripens a week later." In some countries a careful search has already been made for rust-resistant varieties, but on the whole, with comparatively little success from the economic point of view. This partial failure has not been due so much to the difficulty of finding relatively immune varieties, as to the difficulty of finding immunity in combination with other features essential for the profitable cultivation of the crop. Knight[1] appears to have been one of the first to realise the necessity of the "formation or selection" of resistant varieties, and from time to time the attempt has been made. The researches of the late William Farrer may be quoted as an example[2]. The problem has proved an exceptionally difficult one, and even Farrer's patient work has not met with the success one hoped it would. Now, however, that we are in the possession of the broad outlines of the inheritance of the more important characteristics of wheat, the attempt to combine in one variety such features as quality, proper time of ripening, cropping power and so on, together with immunity to the commoner rusts, may profitably be made. Such attempts will have to be made in each country where wheat is cultivated; for wheats suitable for English conditions will certainly find no favour in Canada or Australia for instance. Under such circumstances it would be useless for a breeder, knowing one set of conditions only, and that one not particularly suitable for experiments of this kind, to attempt to do more than indicate the mode of attack which appears to be most suitable. In the first place, the varieties most suitable for the locality will have to be selected for crossing with any which are found to be more or less rust-resistant. From Eriksson's researches it is clear that some varieties are resistant to one rust but not to others, and where this particular rust happens to be the serious one locally, such a variety may be used for breeding experiments. There is, however, one wheat which is characterised by exceptionally complete immunity to the attacks of the

[1] Knight, *The Pamphleteer*, Vol. VI. p. 402, 1815.

[2] Farrer, *Agric. Gaz. of New South Wales*, Vol. IX. p. 131, 1889.

three common rusts—the yellow, black, and brown, namely, *Triticum monococcum* or Einkorn. This primitive type will in all probability prove in the long run the most valuable source of immunity. There is, however, one drawback to its employment for this purpose, that being its complete lack of all the characteristics which go to the building up of a typical bread wheat. Consequently the breeder has to face a somewhat complex problem, but knowing the characters of each of the varieties used as parents, he can calculate the chances of obtaining the combinations required, and by growing sufficiently large cultures of the generation bred from the hybrid, make certain of their occurrence. From the experiments already described it may be inferred that the immunity is transmitted in all its entirety so that any bread wheat with Einkorn as one parent might then be handed on to the other workers to simplify the problem of raising varieties suitable for other districts.

Summary.

On crossing immune and susceptible varieties the resulting offspring is susceptible.

On self-fertilization these susceptible individuals produce immune and susceptible descendants in the proportion of one of the former to three of the latter. The degree of susceptibility is variable.

Where the degree of susceptibility differs in the two parents the hybrid resembles the more susceptible parent in that respect. Among the descendants of such hybrids the two degrees of susceptibility appear in the usual Mendelian ratio of one slightly to three very susceptible individuals.

The relatively immune forms breed true to this characteristic in the succeeding generations.

Immunity is independent of any discernible morphological character, and it is practicable to breed varieties morphologically similar to one another, but immune or susceptible to the attacks of certain parasitic fungi.

NOTES ON THE INFECTION AND HISTOLOGY OF TWO WHEATS IMMUNE TO THE ATTACKS OF *PUCCINIA GLUMARUM*, YELLOW RUST. [WITH PLATE II.]

BY DOROTHEA C. E. MARRYAT.

IT has been known for a long time that there exist varieties of wheats and other cereals which appear to be practically free from, or immune to, the attacks of certain fungal parasitic pests, by which closely allied forms are ravaged.

As far back as 1815, Thomas Andrew Knight suggested that these forms should be carefully sought out and cultivated by farmers[1]. Mr Biffen, on the University Farm at Impington, Cambridge, has for some years past given special attention to this subject. He has discovered and grown several wheats which show to a greater or less degree immunity to the attacks of *Puccinia glumarum*, Yellow Rust. He has further proved that this power of resisting disease behaves as a simple Mendelian character, so that on crossing such wheats with those which, though non-immune, possess other desirable qualities, the latter can be combined with freedom from disease, and a pure race eventually bred[2].

In applying the term "immune" to a plant, it must be explained that this does not signify that it is never attacked at all by the parasite, but rather that the latter is unable to develope normally in such a host, and that since its progress is checked, and spores are never, or only rarely produced, the plant is practically unharmed and infection cannot spread.

The late Professor Marshall Ward and Mr Evans a few years ago examined the histology of one of these wheats, but published only a very brief account of the results which they obtained, without giving any figures[3].

[1] *Pamphleteer*, Vol. VI. p. 402.

[2] Biffen, *Journal of Agricultural Science*, Vol. I. p. 40.

[3] Marshall Ward, *Annals of Botany*, Vol. XIX. p. 35.

Since then, several wheats have been discovered by Mr Biffen which display a considerably greater degree of immunity than the one then used (Rivet Wheat). I have recently examined several of these and here give a rather fuller account of the phenomena observed.

Two forms were used for experiment: (i) *American Club* (a variety of *Triticum compactum*) obtained by Mr Biffen from Mr A. E. Humphries, who found it growing in a plot raised from a commercial sample of N. Duluth wheat, together with several other varieties. (ii) *Einkorn* (*Triticum monococcum vulgare*, Kcke), a half-wild form, which except for this character of immunity, is practically worthless from a farmer's point of view. Of these two wheats, *Einkorn* shows in the field an even greater degree of immunity to Yellow Rust than *American Club*, for only in two instances have a few small scattered pustules, which had not broken the epidermis, been found upon its leaves, in spite of the examination of hundreds of plants[1]. For purposes of comparison, cultures were also made of a third form, *Michigan Bronze*, a wheat peculiarly susceptible to the attacks of Yellow Rust.

Details of Infection.

In June 1906 a number of seedlings of these three wheats were raised in flower-pots, in a cool greenhouse. They were covered with bell-jars in order to prevent accidental infection from stray spores. When the young plants were well up, a number of leaves (which were then marked) of each of the three forms, were infected with uredospores from the fresh leaves of adult plants of *Michigan Bronze*, which were literally orange with Rust.

No change was noticeable in the seedlings until the 6th day after infection, when two leaves of *Michigan Bronze*, the highly susceptible form, showed the first signs of disease, namely, pale yellow flecks. On the following day, almost all the *Michigan Bronze* leaves which had been infected showed similar discoloured areas; they were also found on two of the *Einkorn* and three of the *American Club* seedlings.

After this day, the infection continued to spread rapidly amongst the *Michigan Bronze* plants but more slowly amongst those of *Einkorn* and *American Club*.

By the 11th day, the state of affairs was as follows: almost all the *Michigan Bronze* leaves which had been infected—some 39—showed long, yellowish disease areas, whilst on four of these were visible

[1] Biffen, *Journ. Agric. Sci.* Vol. II. p. 112.

numerous small, but distinct, orange pustules. In *Einkorn*, on the contrary, disease areas were found in only 12 out of the 37 leaves originally infected, and these areas were deep yellow or brownish, and quite small. On some of them were noticeable little black flecks, looking as though the leaf-tissue had been scorched with a red-hot needle. There was no trace of pustules.

In the *American Club* leaves, the infection had spread more than in those of *Einkorn*, but here also, the diseased areas were of a deeper yellow, and indeed the leaves looked more unhealthy than in *Michigan Bronze*, although the actual disease areas were larger in the latter. (The reason of this will be understood when the histology is described.) Further, there were no pustules.

Two days later (13 days after infection), all the infected leaves of *Michigan Bronze* except 5 showed numerous well-developed pustules, in spite of which the leaves looked fairly healthy.

In *Einkorn*, the infection had hardly spread at all, only 3 more leaves—making 15 in all out of the 37 originally infected—showing quite small, deep yellow areas. There was still no sign of pustules.

In *American Club*, the disease areas had spread somewhat, and were visible in most of the leaves which had been infected, whilst on one leaf, when examined with a lens, were found a few scattered, feeble-looking pustules, very different in appearance from those seen in *Michigan Bronze*.

By the 16th day, every leaf of *Michigan Bronze* which had been infected, save one, was orange with pustules throughout its length, and stood out in the most striking manner amongst the remaining green leaves upon which spores had not been sown.

In the *Einkorn* plants, little change was noticeable; no more leaves showed signs of infection, and in those in which the fungus had managed to make good its entry, it had apparently received a severe check by the withering and death of the leaf-tissue immediately in its vicinity, and was unable to spread farther. The remaining portions of the leaves attacked, appeared for the most part green and healthy. On the 18th day however, one rather shrivelled leaf showed a few scattered, unhealthy-looking pustules, none of which appeared to have burst the epidermis. The pustules did not spread, and were not observed on any other *Einkorn* leaf.

American Club offered an intermediate case between *Einkorn* and *Michigan Bronze*, for although the infection had spread to a certain extent, and by the 17th day, 10 leaves on about 50 plants showed a few

of the minute scattered pustules already referred to, they were so small and insignificant as to be scarcely noticed unless hunted for, and bore no comparison whatever, either in number or size, to those produced on *Michigan Bronze.* During the next few days they hardly spread at all and had apparently reached the maximum of their development.

The seedlings were finally bedded out in the garden at the Botanical Laboratory and left, to see what their fate would be in the open air. The *Einkorn* and *American Club* plants were arranged in rows between those of the rusted *Michigan Bronze* in order to expose them to every chance of further infection.

When examined in August—about 2 months later—it was found that the leaves of the *American Club* plants showed quite a number of pustules, but that these were not bright orange as in *P. glumarum*, but of a burnt-sienna colour, and were probably due to Black Rust, *P. graminis*, a fungus to which this wheat is not immune, but which since it appears much later in the season than *P. glumarum* does not so seriously affect the crops[1].

Michigan Bronze showed a quantity of the familiar orange pustules of *P. glumarum* on most of its leaves, but mixed with these were also the darker pustules of *P. graminis*. The *Einkorn* plants appeared to have developed no pustules of any kind.

It may at this point be emphasized that these results were obtained with "immune" wheats, when the fungus was given a much better chance of successful development than it would normally have in the field. For in the first place there was a liberal sowing of spores, secondly the infected plants were not only seedlings, but were further weak and much drawn from being grown under glass and consequently less able to resist the attacks of the parasite, thirdly the warm damp atmosphere in which the plants were reared was highly favourable for the germination of the spores and their further development.

Histological details.

Infected areas of all three wheats were cut off at different stages and fixed in Chrom. Acetic solution. Sections were cut with a microtome and stained with Diamant Fuchsin and Light Green. Before describing the abnormal condition of the fungus found in the immune wheats, I will give a short account of its normal development as observed in the susceptible form *Michigan Bronze*.

[1] Biffen, *Journ. Agric. Sci.* Vol. II. p. 113, note.

The uredospores when lying on the surface of the leaves, send out from their germ-pores, germ-tubes, which penetrate into the host through the stoma, and swell out in the spaces beneath the latter into what are known as *sub-stomatal vesicles*. Into these pass the nuclei of the spore. (Fig. 1.) From the sub-stomatal vesicles proceed *infection-tubes* or short hyphae, into which the nuclei pass, and which quickly grow out towards the host cells. (Fig. 2.) The next stage is the production of *haustoria* or suckers, which the young hyphae drive into the host cells, and by means of which they obtain their nutriment. The original nuclei of the hyphae meantime divide rapidly[1].

Successful entry being thus effected, the hyphae increase in size, branch, and spread quickly in the tissues of the host, applying themselves closely to the cells and piercing them by means of numerous haustoria. (Fig. 3.)

In these early stages of the normal life-history of the fungus, three things may be specially noted for comparison with the abnormal development in the immune wheats to be described later.

(i) The *numerous nuclei* present in the hyphae, which take up the red of the double stain and shine out very clearly, the hyphae themselves staining green.

(ii) The *large number of haustoria* sent out by the hyphae into the host cells in their vicinity, two or more being often projected into the same cell.

(iii) The *healthy condition of the host cells*, which are for the most part unshrunken, and well-supplied with chlorophyll-granules, bearing out Professor Marshall Ward's remark that "a Uredine when flourishing in a leaf does not act as a devastating parasite, but as one which slowly taxes its host and even stimulates the cells for some time to greater activity[2]."

The fungus continues to spread rapidly throughout the leaf until about the 10th or 11th day, when small hyphae begin to mass themselves beneath the epidermis, preparatory to the formation of pustules. The nuclei now arrange themselves in pairs along the length of the hyphae, which become divided up by septa. Before long, the proximal end of each hypha begins to swell, assumes a more or less oval shape and is finally abstricted as a uredospore. That end of the hypha from

[1] The hyphae of *P. glumarum* are unusually large, varying from 3 or 4 to as much as 18 μ in diameter. They are also characterised by showing but few septa and possessing very numerous nuclei.

[2] Marshall Ward, *Annals of Botany*, Vol. XVI. p. 299.

which the spore has been cut off then begins to swell up to form another, and so on until a whole mass are produced, which soon rupture the epidermis and escape, to repeat the life-cycle when they fall upon a suitable host leaf. (Figs. 4 and 5.)

The young spores, before they are abstricted, stain dark green, and usually show the two red nuclei very beautifully (Fig. 4), but as they mature, they become filled with the oleaginous granules which give the pustules their bright orange colour; the spores then stain dark red, and the nuclei can generally no longer be made out. Germ-pores, through which the germ-tubes will later be put out, are visible in the ripe spores. (Fig. 5.)

It has already been stated that by the 12th or 13th day the *Michigan Bronze* leaves were covered with pustules. These present in section a very characteristic appearance. The tangles of green hyphae from which have been cut off countless red spores, stud and finally burst both the upper and lower epidermis. (Fig. 6.)

After this sketch of the normal development of the fungus, the condition of the hyphae in the immune wheats may be considered. *Einkorn*, as offering the more extreme case, will be described first.

Entry takes place as usual through the stoma, but almost from the beginning the contents of the hyphae look watery and show very few nuclei or merely finely-granular red-staining areas, which perhaps consist in part of broken-down nuclei. (Fig. 7.) Still more striking than this unhealthy appearance of the hyphae is the fact that they appear too feeble to send out any haustoria, for only in a single instance were two very minute ones observed. (Fig. 8.) Already, even in the early stages, the host cells in the vicinity of the fungus look shrunken and contain few chlorophyll granules, whilst in some places, they are already beginning to break down. Rather later stages show parts of the leaf-tissue reduced to a dead shrivelled mass, in the midst of which lie numerous large hyphae, apparently also dead, and stained a uniform deep red. (Figs. 9 and 10.)

Such completely dead areas correspond no doubt to the scorched-looking flecks already noticed on the growing leaves. And it is the more striking to observe them in section after section when one reflects that in a normal case of infection, the leaves would by this time be a mass of pustules.

A word may here be said as to the characteristic manner in which these dead hyphae take up the red stain. It is undoubtedly due to the lack of sufficient nutriment and the consequent formation of oil drops

and other fatty products of starvation. For it has been shown that if the hyphae in an ordinary "non-immune" wheat are starved by cutting off the carbohydrate supplies of the host, they also become highly-granular and stain deep red in the manner described above[1].

It has been mentioned that on one single leaf of *Einkorn* a few pustules were formed. Sections of this leaf proved very interesting. Several normal, though rather small pustules were found, but not even the healthiest-looking had managed to burst the epidermis. Mingled with them were numerous "attempts" to form pustules, if one may so speak, attempts which had obviously proved unsuccessful. The weft of hyphae composing such abortive pustules, was in most cases very small and confused, and instead of being close beneath the epidermis, lay deep down in the leaf-tissue. Moreover the spores, if spores they can be called, were very small and ill-shaped and scarcely recognisable as such. (Fig. 11.)

To sum up, it seems that in this immune wheat, although the fungus manages to make good its entry, to produce comparatively large and numerous hyphae, and even in rare cases to arrive at the production of spores, it is sooner or later starved to death by the breaking-down and death of the host tissue in its vicinity and is able to make no farther progress. The host itself, on the other hand, having checked the ravages of its enemy, continues to flourish, except for these small dead areas.

American Club, as already remarked, offers an intermediate case between *Michigan Bronze* and *Einkorn*.

Here again entry takes place normally through the stomata, with the formation of sub-stomatal vesicles etc. Many of the hyphae at first appear perfectly healthy, in that they stain green and show a number of nuclei. Some of them also succeed in putting out quite healthy, normal haustoria, though these are very much fewer in number than in *Michigan Bronze*, and may sometimes be very small.

Before long, however, this successful progress of the parasite is checked. The nuclei of the hyphae appear to become smaller and to degenerate, and the whole contents become highly granular and stain deep red. Such hyphae present a very striking appearance as they lie amongst the green-stained host-cells, and are followed up in section after section. Sometimes one half of a hypha may still stain green and show nuclei, whilst the other half has already begun to undergo this process of degeneration and stains red. (Fig. 12.)

[1] Marshall Ward, *Annals of Botany*, Vol. XIX. p. 39.

Or, again, even hyphae which have managed to put out haustoria may become filled with small granules and their outlines appear so faint and indistinct that they seem on the road to complete disintegration. (Fig. 13.) The host-cells in such cases often appear moderately healthy. But in other portions of the leaf one may find hyphae which are still flourishing, whilst the host-cells in their vicinity are gradually dying in response to a too vigorous onslaught on the part of the parasite. (Fig. 14.)

In other cases, long, highly-granular hyphae stained a deep red are to be seen lying amongst empty, shrunken host-cells (Fig. 15); rarely, hyphae stained a uniform red are found amongst completely broken-up, shrivelled tissue, a condition already described as characteristic of *Einkorn*.

In a word, in *American Club* one is much more conscious of a continued struggle going on between host and parasite than in *Einkorn*, where the rapid breakdown and death of the host tissue in the parts attacked involves the death of the parasite, and thus soon puts an end to the contest.

The invading fungus is by no means flourishing in *American Club*, but though baulked at one point it manages to hold its own at another, until it finally succeeds in forming a moderate number of small, scattered pustules.

Examined in section, however, only a relatively small number of these are found to produce normal spores which succeed in bursting the epidermis. The remainder exhibit for the most part all stages of abortion (Fig. 16), or, if good spores are produced, they do not succeed in bursting the epidermis, and being thus unable to escape, are practically harmless.

Conclusions.

The mutual condition of host and parasite in these immune wheats —as seen on cutting sections—has now been described. And it has been shown that, though the fungus succeeds in making good its entry and producing hyphae, further progress is either completely checked by the breaking-down and death of the host tissue locally accompanied by the starvation and death of the parasite, as in *Einkorn*, or else a more protracted struggle takes place, as in *American Club*. In the latter case the development proceeds to a farther point but is still greatly retarded as compared with a normal case such as *Michigan Bronze*.

But the *reason* of this immunity is still to seek.

It was thought at one time that it might lie in certain structural peculiarities of such wheats, *i.e.* the thickness of the cell-walls, the size and number of the stomata, the nature of the hairs on the epidermis, etc. Professor Marshall Ward has proved by a long series of experiments that no connexion whatever is found, if the curves of such factors are plotted out and compared with what he has termed "infection curves[1]."

We are therefore forced to fall back upon the theory that immunity to disease is due in these cases to the production of certain toxins and anti-toxins by host or parasite or both, which are mutually destructive.

When the problem as to the nature of toxins and anti-toxins has been more completely solved, and more perfect means of isolating them in plants have been devised, some knowledge as to the reason of immunity may be forthcoming. At present one has to be content with a description of the outward and visible effects of immunity, without being able to explain the more subtle cause.

In conclusion, I may say that it was at the late Professor Marshall Ward's suggestion that this investigation was undertaken, and owing to his kindness that I had the privilege of working in his laboratory. I should like to take this opportunity to thank Mr Biffen for kindly supplying me with material and also helping me with advice.

CAMBRIDGE BOTANICAL LABORATORY.
November, 1906.

EXPLANATION OF FIGURES IN PLATE II.

All the figures except 7 and 10 were drawn with the camera lucida under a $\frac{1}{6}$ objective (×350) and a 2 eye-piece (×8) [Beck], from longitudinal sections of infected leaves, cut with a microtome and stained with Diamant Fuchsin and Light Green.

Figures 7 and 10 are slightly diagrammatic sketches, based upon camera lucida drawings under a $\frac{2}{3}$ objective (×40) and a 2 eye-piece (×8) [Beck].

Fig. 1. Germ-tube, from which the spore has broken off, piercing a stoma, and swelling out beneath into a sub-stomatal vesicle. The latter shows 2 nuclei. (*Michigan Bronze*, 8th day culture.)

Fig. 2. Sub-stomatal vesicle putting out infection-tube or first hypha. The latter shows 4 nuclei. (*American Club*, 13th day culture, a late entry.)

Fig. 3. Older, branched hypha, showing numerous nuclei and penetrating the host-cells by means of haustoria. (*Michigan Bronze*, 7th day culture.)

[1] Marshall Ward, *Annals of Botany*, Vol. XVI. p. 302.

Fig. 4. Young pustule, showing uredospores, each with 2 nuclei. (*Michigan Bronze*, 1th day culture.)

Fig. 5. Mature pustule showing uredospores rupturing the epidermis and escaping. 'he spores at this stage stain so deeply that the nuclei can no longer be seen, but the erm-pores are visible. (*Michigan Bronze*, 16th day culture.)

Fig. 6. Leaf-tissue studded with pustules. (*Michigan Bronze*, 13th day culture.)

Fig. 7. Long branched hypha which shows no nuclei or haustoria, only slightly granular areas, which stain red. (*Einkorn*, 8th day culture.)

Fig. 8. Short, granular, hyphal branches which have sent out 2 very small haustoria. (*Einkorn*, 8th day culture.)

Fig. 9. On the left is seen the shrunken, dead, leaf-tissue penetrated by hyphae, the whole taking up the red stain, on the right the cells unattacked by the parasite are still normal and stain green. (*Einkorn*, 12th day culture, cp. with Fig. 7, which shows the usual condition found about the same time in a non-immune wheat.)

Fig. 10. Part of a similar "dead" area, showing the large hyphae which stain a uniform deep red. (*Einkorn*, 11th day culture.)

Fig. 11. An abortive pustule. (*Einkorn*, 18th day culture.)

Fig. 12. Branched hypha, one-half still staining green and showing a few nuclei, whilst the contents of the other half have become highly granular and stain deep red. (*American Club*, 7th day culture.)

Fig. 13. Granular hyphae and haustoria undergoing a process of disintegration, outlines of hyphae very indistinct. (*American Club*, 11th day culture.)

Fig. 14. Dead host cell, the walls and chlorophyll granules of which have stained bright red, in contact with a still healthy hypha which has stained green and shows numerous nuclei. (*American Club*, 7th day culture.)

Fig. 15. Long, very granular hypha which has stained deep red, amongst empty, shrunken host cells. (*American Club*, 12th day culture.)

Fig. 16. An abortive pustule of *American Club* (14th day culture).

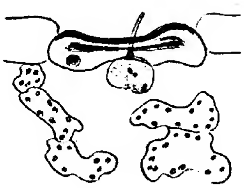

Fig. 1.

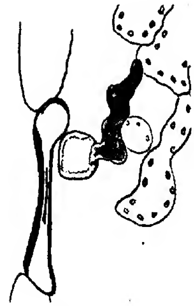

Fig. 2.

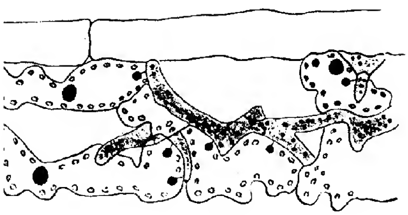

Fig. 3.

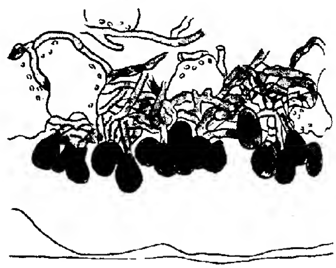

Fig. 4.

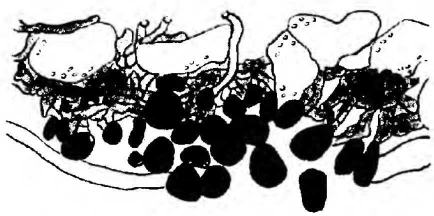

Fig. 5.

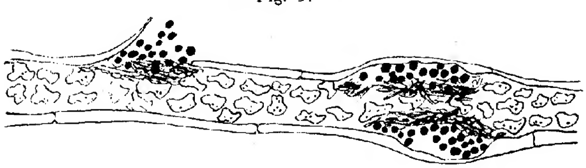

Fig. 6.

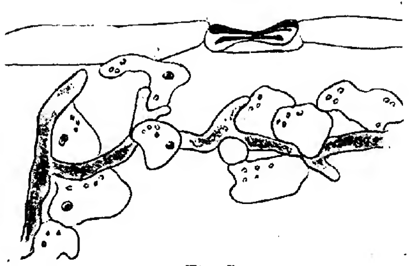

Fig. 7.

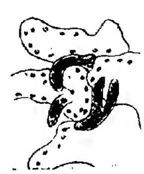

Fig. 8.

Fig. 9.

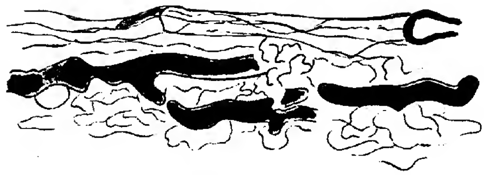

Fig. 10.

Fig. 11.

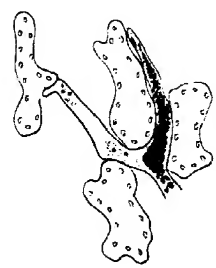

Fig. 12.

Fig. 13.

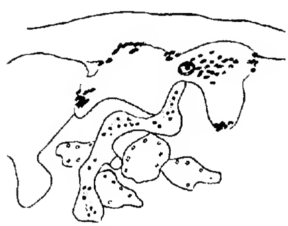

Fig. 14.

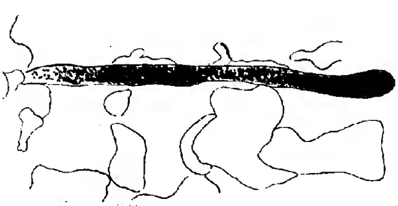

Fig. 15.

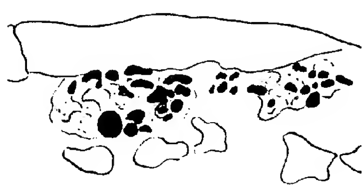

Fig. 16.

THE CHEMISTRY OF STRENGTH OF WHEAT FLOUR.

By T. B. WOOD, M.A.,

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Part I. The Size of the Loaf.

The recent publications of the Home-grown Wheat Committee, and more especially the *résumé* of their work by Messrs A. E. Humphries and R. H. Biffen, which appeared in the last number of this *Journal*[1], have drawn attention to the importance of the wide variation in the baking value of different flours.

The baker likes a flour which will yield a loaf of large size, desirable shape, and good colour and texture, and which can be handled satisfactorily in the state of dough. Another valuable quality to the baker is the power of taking up a large proportion of water in the process of doughing.

It has been the custom, among those concerned with the use of flour, to describe flours which are desirable from the baker's point of view as strong, and since the baker desires so many distinct qualities some confusion has arisen in the use of the term. This was discussed by Humphries and Biffen in the paper referred to above, and the definition of strength they adopt is "the capacity for making large well-piled loaves." Analysing the meaning of this definition it appears that they include in the term strength the separate qualities of size and shape, designedly leaving out the power of absorbing water in doughing, which they quite correctly consider to be an entirely distinct property. Jago[2], on the contrary, defines strength as the capacity of absorbing water, and treats separately the qualities of size, shape,

[1] Humphries and Biffen, *Journ. Agric. Sci.* Vol. II. Pt. I. p. 1.

[2] Jago, *The Science and Art of Bread Making*, London, Simpkin, Marshall & Co., 1895.

colour, and texture. Other investigators are equally at variance in their definitions of strength, and this is perhaps partly the cause of the indefinite state of our knowledge of the chemistry of the subject. In this paper the definition adopted is that of Humphries and Biffen, in which the primary factor is size of loaf, the other factors being shape and, perhaps to a slight extent, texture.

Humphries[1], in his pamphlet on the improvement of English wheat, defines another quality which bakers value, stability, the quality which makes large masses of flour easy to handle in the state of dough. This is an important point in the valuation of wheats, which I hope sometime to have the opportunity of investigating, but which is not touched upon in the present paper.

The best known suggestions for a chemical explanation of strength were mentioned by Humphries and Biffen in the paper already referred to, but it may be well, as this paper deals with the chemistry of the subject, to call attention to them again. The oldest idea suggested that strength was due to the gluten, which, in virtue of its tenacity, or perhaps viscosity, held in the bread the carbon dioxide produced by the yeast. No doubt a high content of gluten is frequently associated with strength, but there are so many cases in which a flour high in gluten is not so strong as another which contains less of that substance, that it can no longer be maintained that gluten content can be considered as a measure of strength. When the quantity of gluten failed to give the desired explanation, attention was turned to the quality of that substance, and it was examined both physically and chemically. The water-holding capacity of different glutens, as measured by the difference between the weight of the wet gluten immediately after extraction and its weight after drying, and the expansion of the gluten when heated to baking temperature in an instrument called the aleurometer, have both been credited with important bearings on the strength of the flour from which the sample of gluten was obtained. No generally accepted regularity seems to have been demonstrated. On the chemical side Girard and Fleurent[2] suggested that strength depends on the presence of a proper proportion of gliadin, which they fix at 75 per cent. of the gluten. Snyder[3] put forward the same suggestion, but fixed his ideal ratio of gliadin to glutenin at 65 per cent. of the former

[1] A. E. Humphries, *The Improvement of English Wheat*, published by the Millers' Association, 56, Mark Lane, E.C.

[2] *Le Froment et sa mouture*, Gauthier-Villars, Paris, 1903.

[3] Minnesota Expt. Stn., *Bulletin* 63, 1899.

to 35 per cent. of the latter. Many other investigators have worked on this branch of the subject, and their results are well summarised in what is practically a monograph on the baking value of wheat flours published last year by Dr F. F. Bruyning, Jr.[1], Director of the State Laboratory for Seed Control in Holland. Finally it has been suggested that it is not the ratio of gliadin to glutenin, but the absolute amount of gliadin in the flour which gives the flour its strength. So contradictory are the results of different workers that the theory that gliadin was the basis of strength has never been generally accepted, and the analyses of Hall[2] in the reports of the Home-grown Wheat Committee, and in his paper in the *Journal of the Board of Agriculture*, have conclusively shown that as often as not gliadin determinations fail completely to indicate whether a flour is weak or strong. In fact Hall[3], in his address to the Millers' Association, goes so far as to suggest that the name gliadin is little more than an "analytical label."

Reviewing the subject as it stands at the present time, it would appear that no one has succeeded in suggesting a generally satisfactory chemical or physical explanation of strength, and no one working on chemical or physical lines has used a definition of the term which does not include at least two distinct properties. Possibly these two facts may be cause and effect. The excellence of Humphries and Biffen's definition as a practical basis for the point they had in view is shown by the striking results Biffen has obtained in breeding new wheats which combine the vigour of the best English varieties with the strength of such foreign sorts as Fife, but even their definition includes two qualities, size and shape of loaf, which are quite likely to be chemically and physically entirely independent, and for each of which a separate explanation must consequently be sought.

Composition of Gliadin.

The peculiar physical properties of gliadin, as described by Osborne and Harris[4], suggest very strongly that it must have a considerable influence on strength, probably on the shape and texture components of that complex idea. As it had already been shown that neither the absolute percentage of gliadin in the flour, nor the ratio of gliadin to

[1] "La valeur boulangère du Froment," *Archives Teyler*, II. IX. 3, 4.

[2] *Journ. of Board of Agr.* XI. 1904, p. 321.

[3] *Report of Home-Grown Wheat Committee*, 1905–6.

[4] *Journ. Amer. Chem. Soc.* XXV. 1903, p. 343.

total proteid, gave satisfactory indications of strength, it seemed possible that as Hall suggested, gliadin might not be a definite substance, or that at any rate the gliadin of very strong flours might differ from that of very weak flours.

The composition of gliadin has been studied by Osborne and Harris, who have hydrolysed it with acids, and investigated its splitting products. They have also determined, by a modification of Hausmann's method, the percentages of amide-, diamino-, and monamino-nitrogen, which it contains. On reading their papers it appeared that their material had been made by extraction of several flours, all of which however must be classed as strong. It was possible therefore that some information might be obtained from a similar examination of gliadin made from a weak flour. Accordingly a quantity of gluten was washed out of two flours, *A* marked 95 for strength, and *B* marked only 40. The two samples of gluten, and also the two samples of flour, were extracted with 70 per cent. alcohol, and samples of gliadin made from each, and purified as described by Osborne and Harris. Approximately 1 gm. of each sample was then boiled for 8 hours with 30 c.cm. of strong hydrochloric acid, the resulting solutions evaporated to dryness, and steam distilled with magnesia into N/10 acid. The results are given below:

TABLE I.

Reference No.	Source of gliadin	Weight taken	c.c. N/10 acid neutralized	Per cent. amide nitrogen in sample of gliadin	Per cent. total nitrogen in sample of gliadin	Per cent. amide nitrogen calculated to pure gliadin containing 17·66 per cent. total nitrogen	Per cent. a[…] nitrogen fo[…] in pure gli[…] by Osbo[…] and Harr[…]
		Grams					
A	Flour	0·9780	29·0	4·16	16·74	4·40	
	Gluten	0·9770	30·55	4·38	17·16	4·51	4·30
B	Flour	0·9692	27·9	4·03	16·51	4·31	
	Gluten	0·9936	31·0	4·37	16·92	4·55	

The same problem was also attacked indirectly in the following way. Samples of gluten were washed out of six different flours, dried, and ground. Each was then hydrolysed, as in the case of the gliadin described above, and the percentage of amide nitrogen determined. The percentage of total nitrogen in the flours was determined by Kjeldahl's method, and the percentage of gliadin by extracting 16 gms. with 100 c.cm. of 70 per cent. alcohol, and determining the nitrogen in

20 c.cm. of the solution. The percentage of gliadin in the total nitrogen could then be calculated. The percentage of nitrogen in the gluten was also determined. Taking Osborne and Harris' figures, 17·6 per cent. total nitrogen in pure gluten, and 3·30 per cent. amide nitrogen in pure glutenin, and the mean of my own figures 4·44 per cent. of amide nitrogen in pure gliadin, the figures in the following table have been calculated:

TABLE II.

rce of ten. rence), of our	Bakers' marks of flour	Percentage in flour		Percentage gliadin nitrogen of total nitrogen	Percentage found in gluten samples		Percentage amide nitrogen in pure gluten calculated from	
		Total nitrogen	Gliadin nitrogen		Total nitrogen	Amide nitrogen	direct estimation	gliadin ratio in total proteid
	95	1·69	1·01	60	13·0	3·10	4·19	4·08
	80	2·44	1·23	50	12·1	2·69	3·91	3·87
	80	2·19	1·10	50	10·5	2·40	4·02	3·87
	(75)	2·32	1·15	49	10·7	2·45	4·02	3·86
	63	1·34	·62	47	11·9	2·57	3·80	3·84
	40	1·86	1·01	54	12·2	2·71	3·91	3·91

The results given in Table I. show that the amide nitrogen obtained by hydrolysing gliadins from typical strong and weak flours agree within the limits of error of the method, and the strong presumption therefore is that there is no difference in chemical composition between the gliadins of different flours. In the last two columns of Table II. the percentages of amide nitrogen in the gluten of six different flours as found by direct estimation are compared with the percentages calculated from the percentages of gliadin and glutenin in the different flours on the assumption that both these substances contain constant percentages of amide nitrogen. The figures so arrived at are found to agree as well as could possibly be expected, and there seems every probability therefore that the assumption as to the constant composition of the glutenin and gliadin of different flours is correct. The agreement would have been closer if the gliadin-glutenin ratio had been corrected for the small amount of proteid in the flours which is not either gliadin or glutenin. Such a correction would have slightly raised all the figures calculated from this ratio.

The second, third and fourth columns of Table II. clearly confirm

the conclusion of Hall and others already referred to, that neither the percentage of total nitrogen or of gliadin in the flour, nor the ratio of gliadin to glutenin, can be taken as indicating strength in flours which, like the above, were not grown under similar conditions.

Investigation of the nitrogenous compounds in flour, either from the point of view of their relative proportions, or from that of their chemical composition, does not seem likely to throw light on the meaning of strength, and it was therefore necessary to take up some other line of enquiry.

The Water-soluble Constituents of different Flours.

Having obtained nothing but negative results from the chemical examination of the gluten proteids, the next step was to turn to their physical properties. It is well known that the presence of exceedingly small amounts of salts, acids, or alkalis, may greatly modify the physical properties of proteids with which they are in contact. It seemed possible therefore that an examination of the water extracts of a number of flours of known baking properties might throw light on the question. For this purpose 100 grams of each of six flours were shaken for three hours with 1 litre of distilled water. The acidity of the extract was first measured by titrating 400 c.cm. with N/10 sodium hydrate solution in the presence of phenolphthalein. Using these proportions, the extract of highest acidity required 11·7 c.cm., that of lowest acidity only 4·4 c.cm. There was therefore a large difference in acidity, but these two extremes were found in flours having the same baking strengths. The intermediate acidities showed no relation to the strength of the flours from which they were made. These observations quite confirm those of Hall and others, and acidity does not appear to be related to strength.

Before beginning to estimate the soluble salts chemically I thought it would save trouble to get a rough idea of the total relative amounts of electrolytes in solution in the different extracts by determining their electrical resistances. Measurements were carried out, and indicated great differences in content of soluble salts, but no agreement with baking marks. For instance the highest resistances were given by the extracts of two flours marked respectively at 95 and 66, and the lowest by a flour marked at 80.

This was more or less what I expected, as the physical effect of salts on the proteid would probably depend rather on the ratio of salt to

proteid than on the absolute amount of the salt or salts, and from the rough measurements made there seemed to be some evidence of this ratio running parallel with the baking strength. The chemical examination of the soluble matter of the extracts was therefore proceeded with.

The method adopted was as follows: 100 c.cm. of each extract was evaporated to dryness, dried in the water-oven to constant weight, and weighed, to determine the total soluble solids. The residue was ignited, and weighed to determine the soluble ash. A duplicate set of determinations was then carried out with 500 c.cm. of extract. The ash of this larger quantity was dissolved in excess of N/10 acid, and back-titrated with N/10 alkali, using methyl orange as indicator, to determine the alkalinity of the ash, which was calculated as percentage of K_2O in the flour. Phosphoric acid was finally determined in the solution resulting from this last operation. Soluble nitrogen was determined in 50 c.cm. of extract by Kjeldahl's method. The results of this examination are tabulated below:

Table III.

Reference No. of flour extracted	Bakers' marks	Per cent. total nitrogen in flour	Percentages of soluble constituents of flours					
			Total solids	Ash	Nitrogen	Alkali as K_2O	Phosphoric acid as P_2O_5	Nitrogen- and ash-free extract
K	95	1·88	7·18	0·194	0·506	0·067	0·048	4·11
G	(75)	2·32	4·67	0·261	0·378	0·113	0·079	2·26
I	70	1·62	6·16	0·360	0·370	0·137	0·091	3·70
J	66	1·32	5·82	0·241	0·308	0·109	0·075	3·82
C	40	1·88	4·23	0·243	0·353	0·087	0·074	1·98

The figures given in Table III. show no regular agreement with bakers' marks, nor as already explained was this expected. In Table IV. the ratios of soluble ash, alkali, and phosphoric acid to total nitrogen in the flour are set out.

There seems to be a certain agreement between the ratios shown in Table IV. and the bakers' marks, the stronger flours containing more total nitrogen in proportion to their soluble salt content than the weaker ones, but to this regularity *G* and *C* are marked exceptions. Reverting to Table III., the last column, nitrogen- and ash-free extract,

or, in other words, the percentage of total soluble matter from which have been subtracted the percentage of ash and that of nitrogen multiplied by 5·7 to convert it into proteid, evidently runs parallel with bakers' marks, with the same exception of *G*, the bakers' mark for which is enclosed in brackets. This exception is extremely interesting.

TABLE IV.

Reference No. of flour	Bakers' marks	Ratios to total nitrogen of soluble		
		Ash	Alkali as K_2O	Phosphoric acid as P_2O_5
K	95	9·7	39	39
G	(75)	8·8	28	29
I	70	4·5	16	18
J	66	5·5	16	18
C	40	7·7	29	25

When I received it from Mr Humphries he wrote about its baking properties, "this flour will not make large loaves when baked by itself, but when blended with certain other flours behaves as if it possessed great strength." Here is an indication of two distinct factors, one possibly, one might almost say probably, governing the shape of the loaf, the other governing the volume. The first, on this supposition, would be the ratio of soluble salts to total proteid, or at any rate some factor which modifies the physical properties of the proteid, the second the nitrogen- and ash-free extract. *K* would then be strong because its proteid is in the presence of suitable conditions, and it also contains a high percentage of extract. *I* and *J* would be weak because they fulfil neither of these two conditions so well as *K*. In *G* the condition for good shape is fulfilled, but it cannot make large loaves, and cannot therefore on Humphries and Biffen's complex definition be accounted strong, because it lacks the volume factor, nitrogen- and ash-free extract. The same reasoning applies, though perhaps not so satisfactorily, to *C*. According to the figures in Table IV. it should on the score of ratios of salts to total proteid rank for shape of loaf above *I* and *J*, but it cannot do so in the bakehouse because it is low in the volume factor as shown by the extract figures in Table III.

This idea of separating strength into at least two factors, that of shape and that of volume, each independent of the other, at once seemed likely to be a good working hypothesis. As the volume factor obviously offered the simpler and more direct problem, I have mainly directed my attention to its investigation.

The Loaf-size Factor in Flours.

Soon after making the experiments which have just been described I received from Mr Humphries a sample of flour *L* made from the same kind of wheat as *G* which I had already tried, but of the 1906 crop. The report which accompanied the sample described it as "dingy in appearance, but behaving well in the bakehouse, and capable of making large loaves." Its total nitrogen and water-soluble constituents were at once determined as described above, and compared with those of the same wheat grown in 1905. The results of the comparison are given below:

TABLE V.

Reference No. of flour	Per cent. total nitrogen	Ratio to total nitrogen of soluble			Per cent. nitrogen- and ash-free extract	Remarks
		Ash	Alkali	Phosphoric acid		
G (1905 crop)	2·32	8·8	28	29	2·26	Bakes small loaves
L (1906 crop)	1·90	7·3	23	27	5·22	Bakes large loaves of good shape

These figures are an excellent confirmation of the two factor idea of strength: the flour of the 1906 crop has ratios of salts to total proteids almost identical with those of the 1905 flour, but it also contains more than twice as much nitrogen- and ash-free extract and therefore makes large loaves.

This nitrogen- and ash-free extract seemed therefore to be clearly indicated as the factor governing the volume of the loaf. As already stated it was determined by subtracting from the total soluble solids the sum of the ash and the soluble nitrogen multiplied by 5·7 to convert it into proteid. It is therefore the total soluble matter other than proteids. As to its composition, it is undoubtedly chiefly sugar

of one kind or other, probably mixed with various dextrins or dextrin-like substances. Jago[1] quotes many analyses of wheats and flours showing the presence of sugars, and expressly states that the sugar in the flour as such, together with that formed by diastatic action in the dough, is the source from which the yeast makes the carbon dioxide it produces in the process of fermentation. He does not seem to consider however that the percentage of sugar in any way influences the baking properties, unless for the worse, for he says that high sugar content in a flour indicates unsoundness. Girard and Fleurent[2] have also noticed great variations in the amount of sugar in flours. They state that in samples they have analysed glucose and cane sugar were present, the former varying from 0·09 to 0·81 per cent., and the latter from 0·63 to 1·89 per cent. Balland too[3] finds quite similar variations. Bruyning[4] considers that the sugar present in flours is not a mixture of glucose and cane sugar, but is in great part, if not entirely, maltose. Other investigators find cane sugar in the embryo of wheat, but not in the endosperm. The presence of raffinose in flour has also been mentioned. Halenke and Mosslinger, quoted both by Bruyning and by Konig[5], suggest that the baking value of a flour may be determined by digesting 2 gms. with water for two hours at 60° to 70° C., finally raising the temperature to 100° C., and filtering. Maltose is determined in the filtrate. In good flours they state that the maltose so determined amounts to 10—20 per cent., in bad ones to as much as 40—50 per cent. Their method appears to be rather drastic, and the sugar estimation to be difficult in the presence of all the dissolved starch. It calls attention however to the diastatic power of flours.

Evidently it is well known that flours contain a certain amount of sugar, whether glucose, maltose, or cane sugar does not matter for my purpose, for all are fermentable by yeast. It is also well known that flours in virtue of their diastatic power are able to form more sugar from the starch which they contain so abundantly, and that the sugar so formed, together with that originally present, forms the source from which the yeast makes the carbon dioxide it produces when dough is fermented. Since the size of a loaf depends on the expansion of the dough by the formation inside it of carbon dioxide in the process

[1] *The Science and Art of Bread Making.*
[2] *Le Froment et sa Mouture.*
[3] Quoted from Bruyning's Monograph.
[4] Monograph in *Archives Teyler.*
[5] *Landwirtschaftlich und gewerblich wichtiger Stoffe*, Paul Parey, Berlin, 1898.

of fermentation, or proving as it is called, and since the source of this carbon dioxide is sugar, the chief constituent of the nitrogen- and ash-free extract, the hypothesis that the proportion of this extract in flour influenced the size of the loaf seemed reasonable, and worth working out carefully.

The determination of the extract as described above involves three estimations, and the amount is then only arrived at by difference. An easier and more accurate method of arriving at the required result would be to make determinations of the sugar in the flour after incubation with water under conditions comparable with those to which dough is subjected in the process of baking. The easiest method of all however seemed to be to grow yeast in a mixture of flour and water, and measure the volume of carbon dioxide evolved. After some preliminary experiments this method was adopted, and when carried out as follows found to be quite satisfactory.

Twenty grams of the flour are weighed out into a wide-mouthed bottle, and a suspension of half a gram of yeast in 20 c.cm. of distilled water added and thoroughly mixed with the flour by stirring with a glass rod. The bottle is then closed with a rubber cork through which passes a delivery tube. The gas evolved is collected in a measuring tube, the bottle meanwhile being incubated in a water-bath kept at 35° C.

A convenient arrangement, if many flours have to be tested, is a large water-bath with clips soldered round it to hold a number of bottles, each of which can be connected by a rubber tube to a measuring tube. The differences observed in the volume of gas given off by various flours are so large that the apparatus described is quite accurate enough to measure them satisfactorily. The actual volumes of gas given off in the experiments varied from 345 c.cm. to 131 c.cm.

After a number of preliminary trials of the method with two flours at a time, a large apparatus was made, and the following series tested all at once.

TABLE VI.

Comparison of Bakers' Marks, Volume of Carbon Dioxide, and Size of Loaf.

Reference No. of flour	Bakers' marks	Volume of CO_2 evolved (S = 100)	Percentage total sugar in flour calculated as glucose	Increase in sugar after incubating 3 hours with water at 40° C.	Volume of loaf made from 100 gms. flour (S = 100)
S	85	100	2·3	2·7	100
P	90	94	2·6	0·6	85
O	96	90	—	—	80
L	85	88	2·5	—	88
T	(20)	83	1·8	0·4	81
M	73	79	2·0	0·6	78
N	(96)	77	2·2	0·4	—
Q	68	66	2·5	0·5	—
G 2	(85)	64	—	—	76
G 3	(85)	62	—	—	76
R	65	60	1·9	0·3	70
J	63	59	—	—	60
C	40	48	—	—	—
V	45	45	1·7	0·1	—
U 2	60	45	—	—	67
G	(75)	44	1·6	—	—
U	36	37	1·6	0·4	—

Inspection of the figures in Table VI., and of the curves in Fig. 1, shows at once that there is a general relation between bakers' marks and the volume of carbon dioxide which a flour can give off when incubated with yeast and water. It is clear however that there are several very marked exceptions, for instance, flours *T*, *N*, and *G*. The remaining flours show quite as close an agreement between bakers' marks and volume of gas as could be expected when it is remembered that bakers' marks are given for both size and shape of loaf, whilst gas evolution only deals with size.

The three exceptions were carefully investigated, and the result of the enquiry has given a most interesting confirmation to the idea.

G is the flour already mentioned which could not make large loaves when baked by itself, but when blended with certain other flours behaved as if it possessed great strength. It evidently could not make large loaves because it contained very little sugar, and consequently could give off very little gas. In describing it Mr Humphries wrote, "it seems to lack the something which makes the bread rise." I was

unable to obtain the identical flour with which it blended most successfully, but sample *S* may be taken as the same flour of the 1906 crop. I have also obtained flour made from the same variety of wheat grown

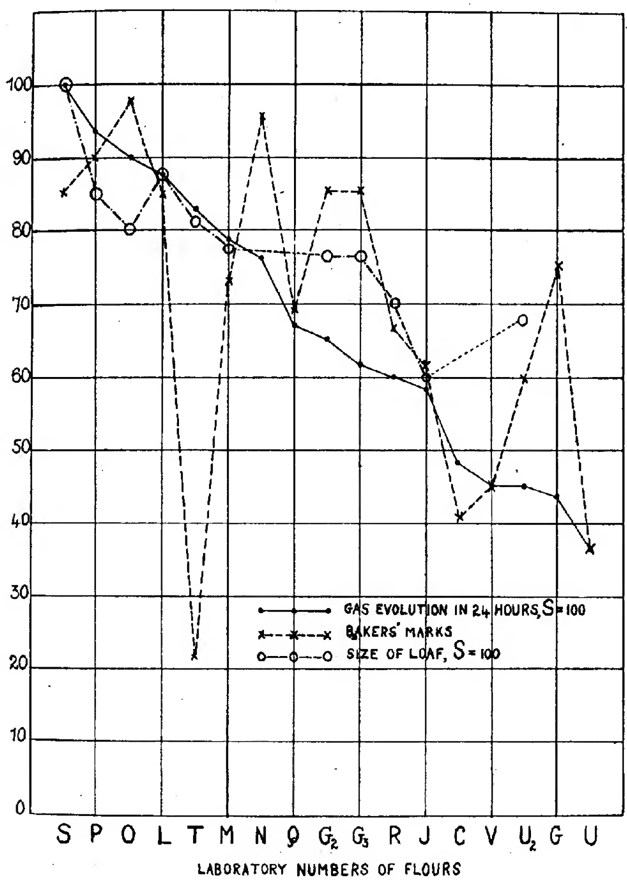

Fig. 1.

in 1905 in another district. Both these flours contained high percentages of sugar, both possessed high diastatic capacities, and both gave off large volumes of carbon dioxide when incubated with yeast.

There seems to be no difficulty therefore in explaining why *G* is an exception. It was evidently marked high on account of its capacity to act as a strong flour in blends, the other flour supplying the sugar in which it is lacking. The two factor idea of strength ought to be of the greatest use in deciding what flours to blend together. The flour *G* was found to give a large loaf when baked with the addition of sugar (Table IX.).

N like *G* is marked much higher than its gas evolution would indicate. On looking up the report which accompanied its marks, I found that it had been baked for marking with the addition of malt extract to the sponge. This would of course increase the diastatic capacity of the flour, and render more sugar available for the yeast, thus supplying the requisite gas evolution for making a large loaf. Unfortunately I had not sufficient material to bake this flour with and without malt extract, and thus definitely settle the point, but it seems quite clear that the high marking was the result of the artificial increase in the volume factor (sugar) by the addition of malt extract, and this exception is therefore brought into line. It is interesting here to note that it appears to be a common practice with bakers to add malt extract to certain flours, usually strong flours in which the shape factor, whatever that may be, is well developed, and thus to increase the size of the loaf. I believe sugar is also frequently used for the same purpose.

T was found on enquiry to be a most interesting case. When I found its gas evolution was altogether too high for its bakers' marks, it at once occurred to me that it might have been kept some time since the baking test was made, during which time it had undergone a large increase in strength, as noticed in the case of the extremely weak flour of some of the Rothamsted permanent wheat plots. I therefore asked Mr Humphries to repeat the test if he thought it likely that such might be the case. He very kindly did so, and reported that in the two months which had elapsed since the last test it had appreciated in strength to a mark of 40. He remarked that it made fairly large loaves of very bad shape. I was fortunately able to obtain more flour, and to bake it myself side by side with a number of others. On measuring the volumes by displacement of small-shot, *T* was found to occupy a place on the list quite in accordance with its relative gas evolution, and this last large exception is thus accounted for, partly by increase of strength on keeping, and partly by actually measuring the volume of the loaf and thus eliminating the shape factor from the

bakers' marking. My own baking experiments were made on a very small scale, but Mr Humphries very kindly repeated them for me in his bakehouse under my own supervision, and allowed me to measure the volume of the loaves. A two-pound loaf of four different flours on the average of two experiments measured: *T* 2294 c.cm., *M* 2281 c.cm., *R* 2086 c.cm., *J* 2012 c.cm. These figures entirely confirm my own small tests, and make the volume of the loaf follow the gas evolution. Very accurate agreement between gas evolution and size of loaf cannot be expected, for two obvious reasons: baking experiments cannot be carried out with any very great accuracy, since the temperature of the oven will vary from one place to another, and all the doughs cannot be put into the oven at what the bakers call the same stage of ripeness, and again the shape factor, whatever it may be, must influence the size of the loaf to a certain extent. The figures for gas evolution and size of loaf in Table VI. and in Fig. 1 follow one another as closely as can be expected, and seem to justify the conclusion that the capacity of a flour for giving off gas when incubated with yeast and water is the factor which in the first instance determines the size of the loaf.

So far as I am aware this factor has not been suggested as one of the components of strength by any investigator. That the idea must have occurred to Maurizio[1] is evident from perusal of an important paper published by him in 1902. In this paper Maurizio describes his investigations of the cause of the variations in the size of the loaf. He apparently did not attempt to test the capacities of the different flours he used to give off carbon dioxide when incubated with yeast and water. His idea was that the size of the loaf might depend on the fermentative capacity of the yeast. He baked loaves with yeasts of varying fermentative capacities, and found that he could establish no relation between the activity of the yeast and the size of the loaf. This is not surprising, as any yeast would produce abundance of gas during the long process of doughing if the flour provided it with enough sugar. In the second part of his paper, a series of experiments is described which bears more nearly on the point in question. These experiments were carried out as follows:—six flours were doughed with appropriate quantities of yeast and water, sugar being added to some in such amount that the volume of carbon dioxide given off in two hours at 30° C. was the same for each flour. These volumes were determined by calculation from the loss in weight of the doughs. The

[1] *Landwirtschaftliche Jahrbücher*, xxxi. 1902.

volume of the dough made without yeast was determined by measurement, and this volume added to the volume of carbon dioxide was taken as the theoretical volume of the dough. The actual volume to which the dough expanded in the process of rising was also measured, and compared with the theoretical volume. The theoretical volumes were approximately equal, varying only from 778 c.cm. to 705 c.cm., a difference of 13 per cent. The actual volumes of the dough varied from 450 c.cm. to 365 c.cm., a difference of 20 per cent. His next step was to calculate a theoretical volume for the bread, from the volume of the carbon dioxide expanded to the temperature of the oven, 250° C., and the volume of the solids of the bread. This is compared with the actual volumes of the loaves and the following variations are found: theoretical volumes 930 c.cm. to 840 c.cm., variation 11 per cent.: actual volumes 502 c.cm. to 290 c.cm., variation 73 per cent.

From these figures Maurizio concludes that gas escapes in the processes of doughing, rising and baking, and that the size of the loaf is therefore not proportional to the volume of gas evolved. These conclusions are obvious from my own figures. For instance I find that in 4 hours, the average duration of my baking experiments from the first mixing of the flour with yeast and water to the end of the baking, Fife flour will give off about 200 c.cm. of gas per 20 grams of flour. 100 grams would therefore give off 1000 c.cm. The size of the loaf baked from 100 grams of this flour is only 320 c.cm. There is evidently therefore a loss of gas amounting to about two-thirds of all the gas produced. Again I find that the volume of gas given off by 20 grams of different flours varies from 345 c.cm. to 131 c.cm., a variation of 163 per cent., as compared with a variation in the size of the loaf from 225 c.cm. to 376 c.cm., or only 67 per cent. There can, therefore, be no doubt either that loss of gas takes place both from the dough and in the oven, or that the size of the loaf is not proportional to the gas evolution, but these facts are quite consistent with the idea that the gas evolution has an effect on the size of the loaf. In his paper Maurizio gives another series of baking tests with the same flours, no sugar being used, and the yeast having about the same fermentative capacity as in the experiments already quoted. The results of the two experiments are tabulated below:—

TABLE VII.

Maurizio's Experiments, with and without sugar.

Flour No.	"Gärkraft" of yeast		Weight of flour in grams	Volume of loaf in c.cm.	
	No sugar experiment	Sugar experiment		No sugar	Sugar added to give off same volume of gas in all cases
1	79·26	85·9	100	458	502
2	"	"	"	425	483
3	"	"	"	419	463
4	"	"	"	398	414
5	"	"	"	311	334
6	"	"	"	251	290
Difference per cent. between smallest and largest loaf				84	73

The figures show quite clearly that by adding sugar to the flour all flours cannot be made to produce equally large loaves, but they also show that the sugar has had an appreciable effect on the size, for without sugar the smallest and the largest loaves differ by 84 per cent. in size, whilst with added sugar the difference is reduced to 73 per cent.

Another important point is that Maurizio by adding sugar adjusted the conditions so that all his doughs gave off the same weight of gas in 2 hours. In this connexion the figures showing rates of gas evolution from 20 grams of flour, 20 c.cm. of water and 0·5 gram of yeast, in my own experiments, are of interest. These figures are set out in Table VIII.

TABLE VIII.

Rate of evolution of gas in c.cm. per hour by different flours when incubated with yeast and water.

Reference No. of flour	1st hour	2nd hour	3rd hour	4th hour	5th hour	6th hour	7th—24th hour
P	44	64	46	35	23	16	5·2
T	44	67	42	22	15	11	4·7
M	54	71	36	17	10	8	4·2
N	47	70	37	17	13	11	4·2
Q	50	60	25	14	13	11	3·0
R	46	54	22	15	12	9	2·7
V	42	39	18	11	9	6	1·9
U	45	34	11	8	6	4	1·3

It is at once evident on examining the figures that all the flours used give off gas rapidly when first mixed with yeast and water, and this rapid evolution lasts for about two hours. During this first period the yeast is presumably using up the sugar which existed as such in the flour. In Maurizio's sugar experiments his added sugar would increase the original rate of gas evolution, but all the sugar would be used up in the two hours' incubation, and when he moulded his loaves and prepared them for the oven, his added sugar would have been

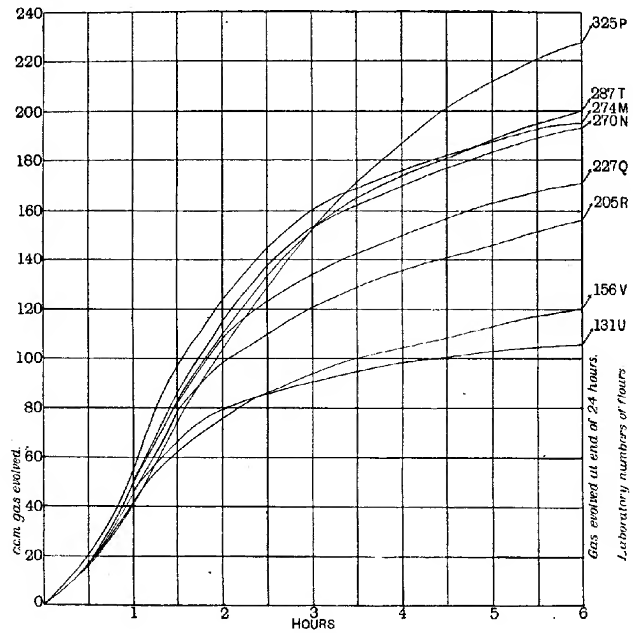

FIG. 2.

used up and the gas produced from it lost. This would certainly be so in ordinary practical baking. The gas which influences the size of the loaf is that which is given off during the later stages of fermentation, when the loaves have been moulded and are waiting to go into the oven. The figures in Table VIII. show clearly that in the case of the four flours *P*, *T*, *M*, and *N*, which make large loaves, gas evolution continues to take place at a sufficient rate to keep up a pressure in the

dough, and counterbalance the leak, even after the sixth hour of fermentation. This gas produced in the later stages of fermentation comes rather from sugar formed by diastatic action than from added sugar, or sugar originally present. In the flours *Q*, *R*, *V* and *U*, which make small loaves, the rate of fermentation becomes very slow in the later stages, so slow that it does not suffice to keep up a pressure in the dough, and the dough therefore becomes flabby, and cannot expand when put into the oven. If Maurizio had added sugar later in the fermentation he would probably have obtained different results, as is shown in the following experiments. These experiments were designed to test the idea that gas-forming capacity is the first factor in determining the size of the loaf. They were carried out as follows: two equal quantities of the same flour were weighed out into porcelain dishes, and warmed to 20° C. An appropriate quantity of water, warmed to 40° C., was measured out, and a weighed quantity of yeast

TABLE IX.

Effect of Added Sugar on the Size of the Loaf.

No. of experiment	Kind of flour used	Weight of flour in loaf grms.	Per cent. sugar added	Volume of loaf without sugar c.cm.	Volume of loaf with sugar c.cm.	Increased volume due to sugar c.cm.	Increased volume per cent.	Rate of gas evolution in c.cm. per minute at time of baking
1[1]	U	56	1	162	170	8	5	—
2[1]	"	56	2	162	180	18	11	—
3[1]	"	56	2	162	190	28	17	—
4[1]	"	56	2	152	176	24	15	—
5[1]	"	50	2	142	141	0	0	—
6[1]	"	280	2	955	1018	63	7	{ 0·6 2·1
7[2]	Household	280	1	985	1035	50	5	—
8[2]	"	280	1	995	1127	132	13	{ 1·7 2·1
9	G	100	5	250	350	100	40	—

[1] Average of three experiments. [2] Average of two experiments.

suspended in it. This yeast suspension was then poured into a depression in the flour, and about one-third of the flour stirred into it so as to make a thick cream, or sponge, as it is called by the baker. This was then incubated at 30° C. for about one hour. At the end of this incubation a weighed quantity of sugar was added to one of the sponges, both were then worked up into dough, and again incubated for

about one hour, when each was moulded into a loaf, put into a tall cylindrical tin, incubated for about half-an-hour, and finally baked in a gas oven at 250° C. During the whole process the two were treated in exactly the same way, except that one had sugar added to it, while the other had not. Tall tins were used to eliminate the shape question as far as possible, and to facilitate measurement of the volume of the loaves.

The figures in the above table show clearly that it is possible to increase the size of loaf which can be produced from flours of deficient gas-producing capacity by the addition of sugar in the later stages of the dough fermentation, a result which confirms the suggestion that the small size of the loaf in such flours is due to lack of gas evolution in the dough. The large increase in the case of the flour *G* is especially interesting in this connexion, as it is the flour of which the 1905 crop fell short of its reputation for strength, in that it could not make a large loaf because of its low sugar content and diastatic capacity (cf. Table V.).

In experiments 6 and 8 the rate of gas evolution at the time of baking was measured in the following manner: 600 grams of flour were weighed out and treated as already described. When the loaves were moulded, portions of dough corresponding to 280 grams of flour were weighed out for each loaf, and a second portion of each corresponding to 20 grams of flour was then put into a bottle connected with a measuring tube, so that the rate of gas evolution could be measured. The bottle was incubated side by side with the moulded loaves while they were rising, or proving as it is called, for baking. In experiment 6 the dough to which sugar had been added was found at the time of baking to be giving off gas at the rate of 2·1 c.cm. per minute, as compared with 0·6 c.cm. in the case of the same dough without sugar. In experiment 8 the corresponding rates were 2·1 and 1·7 c.cm. per minute. In both cases therefore increased rate of gas evolution was associated with increased size of loaf.

Similar measurements were also made in the case of several different flours. The results are given below:

Flour used	S	T	M	U
Relative rate of gas evolution at time of baking	2·0	0·6	0·4	0·2
Relative size of loaf	100	68	69	51

Here too the rate of gas evolution and the size of the loaf run parallel, and it seems certain therefore that it is more particularly the gas given off in the later stages of dough fermentation that determines the size of the loaf. This being so the size of the loaf will depend, not so much on the sugar present in the flour as such, as on the diastatic capacity, which will cause continued sugar formation, and consequently continued gas evolution in the dough. Probably therefore measurement of the gas evolved in the later stages of the fermentation would give a more accurate test for the power of making a large loaf than the measurement which I have made of the total volume given off in 24 hours. This idea corresponds with the view of Hays and Boss[1] who used the "second rise" as a test of the baking value of wheat flours in their breeding experiments. This point is under further investigation.

One further confirmation occurred to me. If the size of the loaf depends on the volume of gas evolved in the dough, then by using a constant weight of baking powder to provide the gas, instead of yeast, all flours should make loaves of approximately the same size. A number of small loaves were baked of flours which with yeast produce loaves of very varying sizes. Figures for these are given in the following table:

Laboratory No. of flour	Size of loaf. S=100	
	Yeast	Baking powder
S	100	100
P	85	106
U	67	107

The experiment is satisfactory as far as it goes, that is to say, in the three cases tested the loaves differ greatly in size when baked with yeast, whilst with baking powder they give loaves which are sensibly of the same volume. It is however difficult to bake presentable loaves with baking powder, and I do not place much reliance on the figures obtained.

In conclusion I have great pleasure in again acknowledging my indebtedness to Mr A. E. Humphries for material and advice, and for kindly permitting me to carry out experiments in his bakehouse. I also have to thank my colleague, Mr R. H. Biffen, for much in-

[1] Minnesota Agric. Expt. Stn., *Bulletin* 62.

formation on the subject of wheats and flours, and Mr W. B. Hardy for advice on the physical properties of proteids and many other points. Messrs F. W. Foreman, G. Evans, and G. G. Chapman have from time to time given me valuable assistance in analytical work.

Summary.

Attention is drawn to the complexity of the ideas comprised in the term strength as applied to flour, and the necessity of investigating each idea separately.

The chemical composition of the gliadin and glutenin of strong and weak flours has been investigated, and it is shown that they are identical in all the flours examined. It is suggested therefore that the difference between strong and weak flours is connected rather with the physical properties of their gluten than with the chemical composition. Since it is well known that the physical properties of proteids are profoundly affected by small quantities of acids, alkalis, and salts, the amounts of these substances in strong and weak flours were determined. In the few cases examined, it was found that strength was associated with a high ratio of proteid to salts, and weakness with a low ratio. It is suggested that the variation of this ratio may be the explanation of the different physical behaviour of the gluten of strong and weak flours, and that this is the factor which determines that component of strength which governs the shape of the loaf, and its power of retaining gas. This point is receiving further investigation.

The factor which primarily determines the size of the loaf which a flour can make is quite distinct. The size of the loaf is shown to depend in the first instance on the amount of sugar contained in the flour together with that formed in the dough by diastatic action. It is proposed to measure this by incubating the flour with yeast and water, and collecting the carbon dioxide evolved during 24 hours. Particular attention should be paid to the rate of gas evolution in the later stages of the fermentation, as this is shown to be more directly connected with the size of the loaf.

Taking Humphries and Biffen's definition of strength as "the capacity for making large well-piled loaves," and applying the above ideas, it is stated that the largeness of the loaf depends chiefly on the capacity of the flour to give off gas when fermented with yeast, especially in the later stages of dough fermentation, and the suggestion is made that shapeliness, and probably gas retention, are dependent on the physical properties of the gluten as modified by the presence of varying proportions of salts.

SOILS OF CAMBRIDGESHIRE.

By F. W. FOREMAN, Univ. Dipl. Agric.,
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INTRODUCTORY NOTE[1].

In 1904, Sir James Blyth, Bart., a member of the Cambridge University Board of Agricultural Studies, offered a Scholarship tenable by a student who had taken the University Diploma in Agriculture, for the purpose of enabling him to spend a year in research. The offer was gratefully accepted, and the Scholarship was awarded to Mr F. W. Foreman. Mr Foreman submitted as a subject for investigation the Composition of certain of the Soils of Cambridgeshire. This subject was approved, and the work was carried out in the winter months of 1904—1905. The results are given in the following pages.

As I was partly responsible for the general plan of the work, I may explain the objects in view. In the first place, we were desirous of obtaining some general information about our local soils. Of recent years, the methods of mechanical analysis have been entirely recast, and it was obviously desirable that we should make use of these methods for the purpose of obtaining the fullest possible knowledge of the soils of the district. In the second place, we were anxious to ascertain whether there exists any close connexion between local soils and the underlying rock formation. On the subject of the relation of soil to rock, a good deal of work was done in the middle of last century, but for 50 years the question has received very little attention in Britain. Thus while both geologists and agricultural chemists have made great additions to their respective subjects, little that is new has been published in this country on the relations of Agriculture to Geology.

The Cambridge district is most interesting to the agricultural geologist. On the north-west and west of the county, and within a

[1] By Professor T. H. Middleton.

few miles of the town, one meets with stretches of Oxford, Ampthill, Kimeridge, Gault, and Boulder Clays; and also with the Lower Greensand, and Glacial and Post Glacial gravels; while the eastern half of the county contains the rich Chalk Marl, the Grey Chalk, the Middle and Upper Chalks, and a second stretch of Boulder Clay. The whole district is intersected by deep ditches and other surface sections, and the subsoils are easily studied. For reasons given in his paper, Mr Foreman did not investigate the whole of this area, but confined his work to the soils lying west of Cambridge.

In working out the relationship of soil and rock, the immediate purpose was to ascertain the accuracy of the information which an agriculturist could obtain from a geological map, and for this purpose, the clay formations in the area selected were particularly suitable. It is obvious that in the absence of surface deposits, a soil on a clay like the Gault must present a marked contrast to the soil on a sand like the Lower Greensand; but it is not so obvious that different clay formations will produce soils having distinctive features. It is not certain, for example, that a Kimeridge clay soil would more closely resemble a Kimeridge clay ten miles away than it would a Gault in the same neighbourhood. If well marked mechanical and chemical characters are to be found in any particular clay, then the geological map would be of great use to the agriculturist who for any reason might wish to obtain a knowledge of the general character of the soils of a district.

The one-inch drift map of the country round Cambridge is, unfortunately, rather old; and surface deposits have not received the same attention that is given to them in the maps now being published by the Geological Survey. Dr Teall, Director of the Survey, kindly offered to place the information in his office at our disposal, but for the preliminary work described in this paper, we did not find it necessary to make use of the six-inch maps. Mr W. G. Fearnsides, M.A., of Sidney Sussex College, gave us the benefit of his local knowledge, and thus enabled us to find typical samples, in different parts of the district, of those soils of which we were in search.

The samples of Boulder Clay were collected in a strip of country about 8 miles long between Haddenham and Hatley; the Gault samples were taken between Landbeach and Harlton, which are ten miles apart; the Greensand samples were taken between Aldreth and Potton, 20 miles apart; the Kimeridge Clays between Haddenham and Lolworth, 10 miles apart; and the Oxford Clays between Abbotsley and St Neots, 4 miles apart. In the last case, samples from other

districts would have been desirable, but in the time at his disposal, Mr Foreman could not deal with a greater number of soils than those described in his paper.

It may be objected that our selected samples representing typical Oxford Clay etc. represent at the same time a condition of things which could not occur in practice, as no surveyor would make a note of all the trifling deviations from the type which might affect the character of the surface soil, for most of these deviations would be without geological importance. There is a good deal of force in this objection; but while it may be admitted that we can never expect the colours of a one-inch map to have a precise agricultural meaning, it is clear that unless we are prepared to sample every field, and thus obtain average figures, that is, unless we are prepared to make an independent soil survey, we must confine our sampling to the type for which the colour stands.

In tracing the relationship between soils, Mr Foreman has made use of four sets of features: (1) the mechanical composition, (2) the chemical composition, (3) the common weeds, (4) the agricultural systems. The two last have been introduced chiefly to supply some facts of general interest about the soils; and the paper is more particularly concerned with laboratory characters. The question we ask is: "Does mechanical or chemical analysis show that any close relationship exists between the soils situated on the same formations?" Taking first the mechanical analyses, we find that they clearly disclose the wide differences existing between the clays and the sands. On the other hand, they sometimes show that very considerable variations occur between soils on the same formation. In the Greensands for example, the clay varies from 2·6 per cent. in soil No. 7 to 12 per cent. in soil No. 16; while in the subsoil of No. 12 (Kimeridge Clay) we have 42·6 per cent. of clay, and in No. 15 26·5 per cent. only. While these variations indicate the necessity for further figures before making general deductions from the analyses, the majority of the mechanical analyses do show a relationship between all the soils on the one formation. All the Gaults for example contain distinctly more fine silt and clay in the surface soil than do the Kimeridge Clays; and with the mechanical analysis of typical Gault before one, it would be impossible to mistake soils Nos. 1, 2, and 4, for Gault although they rest upon this formation, and to the casual observer closely resemble true Gault soils.

Apart from the proportions in which sand and clay are blended, the quality of soil depends chiefly on the quantities of lime, potash,

phosphoric acid, and nitrogen which are present. Of the first three, Mr Foreman gives the percentage found in the soils examined by him, and it is interesting to compare the clay soils in respect of these and other chemical characters. The Oxford is sharply marked off from the Kimeridge and Ampthill clays by the much higher percentage of lime present[1]. All the clays are abundantly supplied with potash, and contain very similar quantities of phosphates. The soils of the Gault contain more lime than those of the Oxford Clay, and containing little visible iron oxide, they differ much in appearance from the Kimeridge Clays.

Even with the limited material which Mr Foreman's work has placed at our disposal, we are justified in concluding that in the Cambridge area the soils are closely related in mechanical and chemical composition to the underlying formations, so that an agriculturist in possession of these analyses would find a good geological map of great use to him. From the agricultural standpoint, a good map is one which indicates the presence of any material that would much modify the character of the soil of any particular formation; such for example as lime, sand, or gravel on clay formations, or of clay on the surface of sandy beds. Mr Foreman's analyses afford illustrations of the kind of information required. Typical Kimeridge clay is very deficient in lime, but here and there thin bands of limestone occur, and when these mix with the soil, they entirely change its character, as is the case with soil No. 17. The agriculturist would therefore wish that the surveyor in mapping clays, should notice the smallest limestone deposits. Again, gravels have covered much of the Gault near Cambridge, and the presence of even small quantities in the surface have greatly modified the clay soils near Impington. See page 172. These gravels may have disappeared, and may only be traceable in pockets, or by pebbles in the surface soil, so that they may have no geological importance. But an indication of their presence on the map would put the agriculturist on his guard, and thus enhance the value of the map.

In drift-covered areas, the agriculturist cannot expect geological maps to have the same value to him as where drift is absent, but Mr Foreman's analyses show that in the case of the Boulder Clay lying west of Cambridge, the only notable difference between the soils is in the percentage of lime which is present; and the very different

[1] One Kimeridge clay does contain lime. For this there is an explanation. See page 173.

types found in soils Nos. 14 and 19 would at once be suggested if the map indicated that one Boulder Clay was chalky while the other was not. T. H. M.

THE DISTRICT INVESTIGATED.

In the neighbourhood of Cambridge the following strata are represented:

- Recent Alluvium
- River Gravels
- Boulder Clay
- Cretaceous :—
  - Chalk
    - Upper
    - Middle
    - Lower
  - Cambridge Greensand—(at one time dug for coprolites)
  - Gault
  - Lower Greensand
- Jurassic :—
  - Upper Oolites
    - Kimeridge Clay
  - Middle Oolites
    - Corallian
      - Ampthill Clay =
        - Coral Rag
        - Coralline Oolite
      - Lower Calcareous Grit
    - Oxford Clay

In collecting soils from these formations some care is necessary. In many cases the one-inch drift map only serves as a general guide to the character of the surface soil. Gault for example may be mixed with Gravel or Boulder Clay, at the surface, or the soil of a Greensand may be mixed with Kimeridge Clay. The analyses given below, except Nos. 1, 2, 4, and 17, represent the composition of typical soils. For advice and assistance in selecting samples I am indebted to the kindness of Mr W. G. Fearnsides, M.A.

At the time of sampling notes were made upon aspect, elevation, drainage, the system of farming and the characteristic weeds. The agricultural information was usually obtained from the farmer himself.

The depth to which samples were taken varied slightly in different cases; the surface soil was sampled to its full depth, and the subsoil to a further depth of seven inches unless its character changed before this depth was reached.

The following is a list of the samples collected:

Reference No.	Formation	Parish	Survey No. of field or local name	Owner	Occupier
1	Gault	Impington	48	Mr J. Unwin	Mr J. Unwin
2	,,	,,	62	Mr J. T. Horrocks	Mr J. T. Horrocks
3	,,	Landbeach	'Old Hole'	Worts' Charity	Mr Hy. Cranfield
4	,,	Impington	39	Mrs W. Millar	Mr W. Millar
5	Lower Greensand	Gamlingay	—	Downing College	Mr Hy. Dew
6	Ampthill Clay	,,	140	Capt. Duncombe	Mr Plowman
7	Gault	Harlton	'Poundgate piece'	Christ's Hospital, London	Mr C. Whitechurch
8	,,	Madingley	79	Trinity College	Mr P. Papworth
9	Lower Greensand	Oakington	'Cottenham Field'	Mr J. H. H. Linton	Mr I. Cock
10	Oxford Clay	Abbotsley	67	Capt. Duncombe	Mr Wm. Rothery
11	,,	,,	101	,,	,,
12	Kimeridge Clay	Oakington	'Cuckoo Hill'	Mr J. H. H. Linton	Mr I. Cock
13	River Gravel	,,	'Peas Hill'	,,	,,
14	Boulder Clay	Hardwick	'Home Field'	Mr J. Hodson	Mr J. Hodson
15	Kimeridge Clay	Lolworth	2	Clare College	Mr J. Mitham
16	Lower Greensand	Oakington	173	Queens' College	Mr W. C. Cole
17	Kimeridge Clay	Haddenham	836	Mr P. A. S. Hickey	Mr A. Hepher
18	Lower Greensand	Aldreth	'Sandway'	Mrs Scott (Ely)	Mr I. Gay
19	Boulder Clay	Boxworth	163	Sir R. P. Cooper	Mr H. Eyre
20	,,	Bourn	'Red House Field'	Lord Clifden	Mr Jas. Broadway
21	,,	East Hatley	113	Downing College	Mr J. E. Ireland
22	Oxford Clay	St Neots	'Twenty-three acre'	Mr G. Fydell Rowley	Mr Rd. Aughton
23	Lower Greensand	Potton	175	Mr Geo. Smith	Mr J. Pibworth

METHODS OF ANALYSIS.

The method employed in making the mechanical analyses of the soils was that recommended by the Chemical Committee of the Agricultural Education Association[1].

Carbonates were estimated by the method devised by Amos[2].

The sizes of the particles aimed at in the mechanical analyses were as under:

TABLE I.

	Diameter in millimetres		Described as	
	maximum	minimum		
Stones and Gravel...	—	25	Stones	Separated by sifting
	25	10	Small Stones	
	10	3	Gravel	
Earth	3	1	Fine Gravel	
	1	·2	Coarse Sand	
	·200	·040	Fine Sand	Separated by subsidence
	·040	·010	Silt	
	·010	·002	Fine Silt	
	·002	—	Clay	

[1] *Journn. Agric. Sci.* Vol. I. Part 4, p. 470.

[2] *Journn. Agric. Sci.* Vol. I. p. 322.

In the chemical analyses the method of extraction employed was that of the Agricultural Education Association as described by A. D. Hall[1].

The phosphoric acid and potash were determined by the method of Neubauer[2] which was found to work very well.

It will be convenient to present the results of analyses in the following order:

Clay soils.	*Sandy soils.*
Boulder Clay	River Gravel
Gault	Lower Greensand
Kimeridge Clay	
Ampthill Clay	
Oxford Clay	

SOILS OF THE BOULDER CLAY.

Boulder Clay covers all the western side of the Cambridgeshire area "capping the high ground on the north of the Rhee valley and spreading in a sheet over the upland region between the valleys of the Ouse and the Cam; and further north a broad mass runs roughly from Kingston to Coton and Madingley, thence in a N.W. direction to Dry Drayton and Lolworth passing through Elsworth and Papworth into Huntingdonshire[3]."

The clay itself consists mainly of a dark grey or bluish mass weathering to a drab or brownish colour to the depth of several feet. The soil directly derived from it has a brownish colour and does not much differ in appearance from the underlying weathered mass. In the subsoil hydrated oxide of iron is visible. The amount of calcium carbonate in the soil and subsoil is nearly the same and runs about 1 per cent.

The soils themselves are extremely tenacious. The season must be very favourable indeed if a satisfactory tilth is to be obtained, and the crops are apt to be mediocre in the best of weather. In the summer wide cracks develop which are ruinous to pastures. When not cultivated the land soon becomes covered over with thorns and it may frequently be seen in a derelict condition. Draining and liming are very beneficial but the cost often makes these improvements

[1] *The Analyst*, November, 1900.

[2] *Landw. Versuchsstat*, 1905, LXIII. 141—149.

[3] Reed, *Geology of Cambridgeshire.*

impossible, amounting to more than the land is worth. The poorest type of pasture is found on undrained Boulder Clay, the roots of the grasses extending only a few inches into the soil, and as the closeness of the texture prevents movements of any kind there is an inadequate supply of air, and a spongy accumulation of undecayed roots collects at the surface.

The following table gives the mechanical analyses of the Boulder Clay soils, all of which were uniform in appearance.

TABLE II.

Mechanical Analysis of Boulder Clay Soils.

	No. 14 Boulder Clay above Gault		No. 19 Boulder Clay above Greensand		No. 20 Boulder Clay above Gault		No. 21 Boulder Clay above Grey Chalk	
	Soil	Subsoil	Soil	Subsoil	Soil	Subsoil	Soil	Subsoil
Depth of sample in inches	7	7	6	7	7	6	6½	6½
Stones, diam. over 3 mm....	2·0	2·4	1·8	1·1	5·0	15·2	2·1	5·3
Fine Gravel	·38	·40	·67	·63	·50	1·07	·86	1·52
Coarse Sand	10·67	10·52	14·79	14·19	14·97	14·03	17·67	16·93
Fine Sand	14·95	14·72	18·55	17·66	15·57	13·87	12·74	14·71
Silt	11·85	12·11	16·37	16·79	12·36	12·05	11·29	11·88
Fine Silt	13·53	13·99	12·35	13·13	12·88	12·18	13·23	12·22
Clay	26·95	29·07	22·28	25·41	28·71	33·00	25·15	28·05
Moisture	3·66	3·44	3·24	3·58	4·40	4·21	4·44	4·46
Loss on ignition (less CO_2) .	9·69	8·51	7·73	6·51	7·78	6·58	10·93	7·31
Calcium Carbonate...........	5·71	4·29	·58	·61	1·35	·99	1·02	1·30
	97·39	97·05	96·56	98·51	98·52	97·98	97·33	98·38

It will be seen that in spite of the fact of a different formation underlying the Boulder Clay, in each case there is a fairly close agreement in mechanical composition. As geologists have pointed out, the Boulder Clay of this district has had the same derivation and the underlying strata do not much influence the composition.

The merging of the rock through the subsoil into the soil is reflected very clearly in the analyses, there being a similar preponderance of the smaller particles in the subsoils and *vice versâ* with the larger particles in the soils.

Chemical analyses of the surface soils were made with the following results:

TABLE III.

Chemical Composition of Boulder Clay Soils.

	No. 14	No. 19	No. 20	No. 21
Moisture	3·66	3·24	4·40	4·44
Organic Matter, etc.	9·69	7·73	7·78	10·93
Insoluble Siliceous Matter	63·87	73·62	70·02	68·01
Lime (CaO)	3·95	·78	1·22	1·325
Magnesia (MgO)	·285	·28	·35	·60
Phosphoric Acid (P_2O_5)	·14	·113	·107	·102
Potash (K_2O)	·948	·785	·994	·963

Here the agreement is more marked than in the mechanical analyses, and it will be observed that all are low in phosphoric acid, high in potash, and fairly high in magnesia.

For comparison with the mechanical and chemical analyses the following agricultural notes are tabulated:

TABLE IV.

Crops grown on Boulder Clay Soils.

No. 14	No. 19	No. 20	No. 21
A better soil than the others, containing more Chalk and Phosphoric Acid. *Crops.* 1900 Barley 1901 Clover 1902 Wheat 1903 Oats 1904 Wheat All fair crops except the last wheat crop which yielded only 20 bushels per acre	A very difficult soil to work. *Crops.* 1898 Mangolds and Vetches (in place of usual bare fallow) 1899 Barley 1900 Oats, manured, but moderate crop 1901 Clover, moderate crop 1902 Wheat, moderate crop 1903 Beans, fair crop 1904 Wheat, manured with 15 loads Farmyard but only 20 bushels per acre owing to bad sowing season	Very difficult to work. *Crops.* 1899 Bare fallow 1900 Barley, 20—24 bushels per acre 1901 Beans, manured with 14—15 loads Farmyard, 12—16 bushels per acre 1902 Wheat, 16—20 bushels per acre 1903 Clover, 1¼ tons hay per acre 1904 Wheat	A very poor pasture which was greatly improved by a dressing of 10 cwt. Basic Slag per acre. See *Journ. Agr. Sci.* I. 125.

The common weeds were:

TABLE V.

Weeds of Boulder Clay Soils.

Specific name	Common name	Remarks
Avena fatua	Wild Oat	Gives great trouble
Ranunculus repens	Kingcob	,, ,, ,,
Brassica sinapis	Charlock	Very abundant
Sonchus arvensis	Sowthistle	,, ,,
Carduus arvensis	Thistle	,, ,,
Carduus acaulis	Dwarf Thistle	,, ,,
Rumex crispus	Dock	,, ,,
Galium aparine	Goose grass	Plentiful
Agrostis stolonifera	Bent	Very troublesome
Daucus carota	Wild Carrot	Fairly numerous
Geranium molle	Dove's foot Geranium	
Plantago media	Plantains	
Veronica agrestis	Speedwell	
Taraxacum densleonis	Dandelion	
Tussilago farfara	Coltsfoot	
Stellaria media	Chickweed	In small quantity
Senecio vulgaris	Groundsel	,, ,,
Ononis arvensis	Rest Harrow	A scourge in the pastures

SOILS OF THE GAULT.

An irregular and fairly wide strip of Gault extends from the S.W. to the E. of the County of Cambridgeshire and thence into Norfolk to Stoke Ferry and beyond. Gault, on weathering, changes to a creamy colour, and gives rise to quite a light coloured soil. No hydrated ferric oxide can be seen. The soils are thus readily distinguished from those of the Kimeridge and Boulder Clays. In this district Gault soils contain a good deal of calcium carbonate which may vary from 3 to 10 per cent. The subsoil nearly always contains a layer of the small rounded chalk pebbles in various stages of disintegration, termed "race" by geologists. In every case a higher percentage of chalk is found in the subsoil after removal of the pebbles than in the soil. Gault soils are very stiff and sticky, but though containing more "clay" are not quite so tenacious as those of the Boulder Clay. The higher content of calcium carbonate modifies the physical properties considerably. Gault soils are very difficult to till, a bare fallow is absolutely necessary at frequent intervals. As a rule it is found however that fair crops can be obtained on these soils in favourable seasons if they are well cultivated.

Three of the Gaults (Nos. 1, 2 and 4) were among the first soils sampled, and as they proved not to be typical, the analyses are given separately. These soils represent a common type, where Gault is mixed with Gravel. They were taken in the neighbourhood of Impington.

The composition of typical Gault soils is shown in Table VI.

TABLE VI.

Mechanical Analyses of typical Gault Soils.

	No. 3		No. 7		No. 8	
	Soil	Subsoil	Soil	Subsoil	Soil	Subsoil
Depth of sample in inches...	5½	6	5¾	6¾	6½	6¾
Stones, diam. over 3 mm....	per cent. 3·4	per cent. 9·0	per cent. 1·0	per cent. ·6	per cent. ·6	per cent. 1·0
Fine Gravel	1·18	1·17	·19	·05	·50	·38
Coarse Sand	18·53	13·01	4·33	1·16	9·87	8·21
Fine Sand	7·08	5·53	4·53	2·30	7·80	7·38
Silt	6·06	6·79	11·97	10·65	10·60	9·23
Fine Silt	13·89	14·68	21·27	18·22	15·57	14·62
Clay	33·04	40·36	31·68	39·96	34·64	38·38
Moisture	4·42	4·86	3·82	4·26	3·14	3·78
Loss on ignition (less CO_2)	10·52	8·28	10·83	7·45	10·51	9·15
Calcium Carbonate	2·05	3·23	8·30	14·71	5·34	8·11
	96·77	97·91	96·92	98·76	97·97	99·24

The increase of the larger particles and decrease of the carbonate of lime as rock passes upwards into soil is again plainly shown in all.

Table VIII. shows the chemical composition of the typical Gault soils.

The percentages of lime and potash are high, while all three soils, and especially No. 8 (a worn-out pasture), are deficient in phosphates.

The agricultural notes relating to the typical Gault soils are given in Table IX.

The common weeds found are given in Table X.

Dandelion appears to be especially favoured by the Gault.

TABLE VII.

Mechanical Analyses of Gault mixed with Gravel.

	No. 1		No. 4		No. 2	
	Soil	Subsoil	Soil	Subsoil	Soil	Subsoil
Depth of sample in inches	5	5½	6	6½	4½	5½
Stones, diam. over 3 mm....	per cent. 1·5	per cent. 1·5	per cent. 1·1	per cent. 1·3	per cent. 4·4	per cent. 3·9
Fine Gravel	·55	·80	1·13	·70	·88	1·48
Coarse Sand	9·43	11·75	12·97	11·70	33·37	26·88
Fine Sand	11·18	11·21	11·35	12·25	14·69	13·48
Silt	18·60	18·73	15·44	14·21	13·40	9·75
Fine Silt	13·63	11·61	13·39	13·13	8·78	7·77
Clay	18·46	20·03	18·43	20·79	14·12	23·50
Moisture	3·74	2·32	3·72	4·03	2·30	2·40
Loss on ignition (less CO_2)	8·92	6·44	8·29	8·32	8·57	7·46
Calcium Carbonate	10·98	11·40	10·28	9·91	1·21	5·22
	95·49	94·29	95·00	95·04	97·32	97·94

TABLE VIII.

Chemical Composition of Gault Soils.

	No. 3	No. 7	No. 8
Moisture	4·42	3·82	3·14
Organic Matter, etc.	10·52	10·83	10·51
Insoluble Siliceous Matter	63·67	56·29	60·35
Lime (CaO)	3·87	7·28	4·74
Magnesia (MgO)	·29	·15	·215
Phosphoric Acid (P_2O_5)	·14	·127	·097
Potash (K_2O)	1·14	1·143	1·30

TABLE IX.

Crops grown on Gault Soils.

No. 3	No. 7	No. 8
Crops. 1901 Wheat 1902 Clover 1903 Barley 1904 Barley again, because owing to bad season wheat could not be sown. Steam cultivated but very light crop. Other crops fair.	1901 Wheat, fairly good crop 1902 Vetches, fairly good crop 1903 Oats, bad sowing-time and poor crop 1904 Wheat, moderate crop	Very worn-out pasture broken up and two crops of oats taken without manure; each yielded about 8 bushels per acre.

TABLE X.

Weeds of Gault Soils.

Specific name	Common name	Remarks
Taraxacum densleonis	Dandelion	Very abundant
Ranunculus repens	Kingcob	,, ,,
Tussilago farfara	Coltsfoot	,, ,,
Carduus arvensis	Thistle	,, ,,
Rumex crispus	Dock	,, ,,
Brassica sinapis	Charlock	,, ,,
Euphorbia peplus	Petty spurge	In smaller quantity
Geranium molle	Dove's foot Geranium	,, ,,
Veronica agrestis	Speedwell	,, ,,
Senecio vulgaris	Groundsel	,, ,,
Potentilla reptans	Cinquefoil	,, ,,
Stellaria media	Chickweed	,, ,,

SOILS OF THE KIMERIDGE AND AMPTHILL CLAYS.

The principal outcrop of the Kimeridge Clay is in the neighbourhood of Ely and Haddenham, a narrow band also runs from Knapwell through Boxworth, Oakington and Cottenham beyond which it spreads out beneath the Fenland of North Cambridgeshire. The Kimeridge Clay consists of dark blue or dark grey clays. Thin layers of limestone in continuous bands or as lines of septarian nodules are found in it, but the clay between these bands is absolutely devoid of chalk; crystals of selenite however are scattered throughout its mass. Except where these thin bands of limestone reach the surface, the soils derived from

the clay are quite devoid of calcium carbonate and in many cases distinctly acid in character.

The clay weathers to a reddish-brown colour and a large quantity of the red hydrated oxide of iron is present. The soils have a dark brown colour, and are quite different from the light coloured Gault and Oxford Clay soils. They are very stiff, sticky, and troublesome, necessitating a frequent bare summer fallow.

The only sample of Ampthill Clay examined was taken from the small outcrop at Gamlingay. Ampthill Clay very closely resembles Kimeridge Clay, and the soil derived from it was similar to those from the Kimeridge in every respect.

TABLE XI.

Mechanical Analyses of Kimeridge Clay and Ampthill Clay soils.

	Kimeridge Clay Soils						Ampthill Clay Soil	
	No. 12		No. 15		No. 17		No. 6	
	Soil	Subsoil	Soil	Subsoil	Soil	Subsoil	Soil	Subsoil
Depth of sample in inches	6	6¾	6½	6½	6	6½	6½	6½
Stones, diam. over 3 mm.	per cent. 1·8	per cent. ·1	per cent. 3·3	per cent. 1·8	per cent. ·1	per cent. 1·0	per cent. ·7	per cent. ·6
Fine Gravel	1·31	·73	1·65	1·54	·29	·47	1·13	1·40
Coarse Sand	21·17	11·58	20·45	20·30	9·98	9·44	19·22	17·37
Fine Sand	12·46	7·33	12·89	11·31	10·67	12·43	8·49	8·37
Silt	14·97	9·80	10·88	11·48	12·79	13·66	16·46	15·68
Fine Silt	11·94	15·18	13·71	14·38	14·39	14·17	14·97	11·38
Clay	28·29	42·68	25·12	26·52	29·87	35·02	24·10	33·36
Moisture	1·62	2·62	3·94	4·54	5·16	4·93	3·70	3·72
Loss on ignition (less CO_2)	7·84	8·10	9·03	7·43	9·28	6·54	10·37	7·20
Calcium Carbonate	nil	nil	·35	·07	3·32	2·18	·204	·09
	99·60	98·02	98·02	97·57	95·75	98·84	98·644	98·57

The only soil which contains chalk in quantity is the Háddenham one, and here, as may be seen from a section in the local brickpits, some thin bands of limestone outcrop and mix with the soil. No. 12 was acid in reaction and Nos. 6 and 15 contained very little chalk.

Table XII.

Chemical Composition of soils of the Kimeridge and Ampthill Clays.

	Kimeridge			Ampthill
	No. 12	No. 15	No. 17	No. 6
Moisture	1·62	3·94	5·16	3·70
Organic Matter, etc.	7·84	9·03	9·28	10·37
Insoluble Siliceous Matter	74·62	71·34	64·22	69·20
Lime (CaO)	·425	·515	2·425	·48
Magnesia (MgO)	·134	·18	·155	·145
Phosphoric Acid (P_2O_5)	·147	·098	·093	·096
Potash (K_2O)	1·13	1·00	1·58	·655

The soils are all poor in lime except No. 17, and all are poor in phosphates and magnesia.

The system of farming adopted upon the Kimeridge Clay soils is shown in the following statement.

Table XIII.

Crops grown on Kimeridge and Ampthill Clays.

No. 12	No. 15	No. 17	No. 6
Crops. 1901 White Clover 1902 Wheat 1903 Linseed * 1904 Oats Field rather exhausted and crops all moderate.	*Crops.* 1901 Wheat, 32 bus. per acre 1902 Fallow, mustard sown in June 1903 Oats, 48 bus. per acre 1904 Swedes, very poor crop, bad tilth. Land unsuited for Swedes.	*Crops.* 1899 Summer fallow 1900 Beans, 28 bus. per acre 1901 Wheat, 32—36 bus. per acre. 1902 Clover 1903 Wheat 1904 Summer fallow	*Crops.* 1901 Oats 1902 Oats 1903 Beans 1904 Wheat, so wet had to sow twice and poorish crop Will grow fair crops as a rule.

* A very unusual crop in this district.

TABLE XIV.

Weeds of the Kimeridge and Ampthill Clays.

Specific name	Common name	Remarks
Avena fatua	Wild Oat	Very troublesome
Tussilago farfara	Coltsfoot	" "
Carduus arvensis	Thistle	" "
Carduus acaulis	Dwarf Thistle	" "
Rumex crispus	Dock	" "
Brassica sinapis	Charlock	" "
Stellaria media	Chickweed	Fairly prevalent
Taraxacum densleonis	Dandelion	" "
Galium aparine	Goosegrass	" "
Veronica agrestis	Speedwell	" "
Geranium molle	Dove's foot Geranium	" "

SOILS OF THE OXFORD CLAY.

The principal outcrop of this formation unobscured by Drift is to the west of the county of Cambridgeshire where it borders with Huntingdonshire. One of the samples (No. 22) came from St Neots,

TABLE XV.

Mechanical Analyses of Oxford Clay soils.

	No. 10		No. 11		No. 22	
	Soil	Subsoil	Soil	Subsoil	Soil	Subsoil
Depth of sample in inches	6½	7	6	7	6¼	6½
Stones, diam. over 3 mm....	per cent. 1·3	per cent. 1·7	per cent. 3·0	per cent. 1·6	per cent. 3·4	per cent. 1·8
Fine Gravel....................	·75	1·16	·85	1·16	1·17	·46
Coarse Sand....................	14·64	13·27	12·33	10·44	15·56	15·15
Fine Sand	7·92	7·91	8·63	7·81	12·86	9·75
Silt	11·67	11·51	14·81	14·24	11·80	7·56
Fine Silt	13·81	14·49	13·40	14·45	12·55	13·39
Clay	29·97	34·96	29·63	30·74	27·16	27·39
Moisture	3·24	2·46	3·25	2·10	4·18	3·72
Loss on ignition (less CO_2)	9·87	7·38	9·99	7·64	7·59	6·66
Calcium Carbonate............	3·04	6·63	4·72	8·90	4·46	11·27
	94·91	99·77	97·61	97·48	97·33	95·35

another (No. 11) from the experimental field of the Cambridge University Department of Agriculture at Abbotsley, which was laid down to pasture in 1900, and the third (No. 10) from an arable field in the vicinity.

In the district mentioned the Oxford Clay itself is a bluish grey clay weathering to a light colour, and the soil and subsoil are not unlike those of the Gault, perhaps a shade darker in colour. The subsoil contains a little hydrated ferric oxide which is just visible. The Clay is distinguished by containing crystals of selenite and nodules of pyrites. At the surface quite a quantity of a characteristic fossil (*Gryphaea dilatata*) is to be found. The subsoil contains small chalk pebbles resembling those in the subsoil of the Gault.

The soils are not quite so sticky as those of a typical Gault, but in all other respects they are much the same. Very little difference can be seen between the subsoil and soil, and the passage upward from rock to soil is not pronounced.

TABLE XVI.

Chemical Composition of Oxford Clay soils.

	No. 10	No. 11	No. 22
	per cent.	per cent.	per cent.
Moisture	3·24	3·25	4·18
Organic Matter, etc.	9·87	9·99	7·59
Insoluble Siliceous Matter	65·01	65·58	67·18
Total Lime (CaO)	3·23	3·22	3·08
Magnesia (MgO)	·215	·47	·25
Phosphoric Acid (P_2O_5)	·118	·145	·138
Potash (K_2O)	1·06	1·11	1·09

These soils resemble each other closely.

The experiments carried out on No. 11 showed basic slag to be a very profitable manure. The soils are intractable, unless dry, and bare fallowing is necessary every four or five years as couch (*Agropyrum repens*) otherwise becomes very abundant.

The following is a list of recent crops and yields:

TABLE XVII.

Crops grown on the Oxford Clay.

No. 10	No. 11	No. 22
1899 Clover, very fair crop 1900 Wheat ,, ,, 1901 Fallow 1902 Barley, very fair crop 1903 Beans ,, ,, 1904 Wheat, very bad crop, bad weather at seed-time	1896 Fallow 1897 Barley, good crop 1898 Beans ,, ,, 1899 Wheat ,, ,, 1900—1904 Pasture	1901 Summer fallow, permanent pasture seeds failed 1902 Wheat, 20 bus. per acre *1903 Oats, 56 bus. per acre 1904 Wheat, 20 bus. per acre (bad seed-time)

* Manured with 15—20 tons mixed London dung and farmyard manure per acre.

TABLE XVIII.

Weeds of the Oxford Clay.

Specific name	Common name	Remarks
Tussilago farfara	Coltsfoot	Very troublesome
Brassica sinapis	Charlock	,, ,,
Ranunculus repens	Kingcob	,, ,,
Carduus arvensis	Thistle	,, ,,
Rumex crispus	Dock	,, ,,
Geranium molle	Dove's foot Geranium	Abundant
Anthemis Cotula	Stinking Mayweed	,,
Sherardia arvensis	Field Madder	,,

SOIL DERIVED FROM RIVER GRAVEL

It will be seen that this is quite a similar type of soil to those of the Lower Greensand. The sample was taken from a field adjoining a small watercourse. This was considered by the occupier to be very good land indeed. The recent crops were:

1901 Barley, good crop.
1902 Peas, good crop, had Farmyard manure.
1903 Wheat, very good indeed.
1904 Barley, moderate crop on account of dry season.

The weeds were very similar to those found on the Greensand soils with, in addition, a very large quantity of what is locally termed "Hardhack" (*Centaurea nigra*).

TABLE XIX.

Mechanical Analyses of River Gravel soil and subsoil.

	No. 13	
	Soil	Subsoil
Depth of sample in inches...	6½	6½
Stones, diam. over 3 mm....	per cent. 9·0	per cent. 10·7
Fine Gravel.....................	2·22	2·40
Coarse Sand.....................	49·80	51·90
Fine Sand	18·14	16·81
Silt	7·20	7·64
Fine Silt	5·90	5·70
Clay	9·74	8·97
Moisture	1·00	·96
Loss on ignition (less CO_2)	5·20	5·12
Calcium Carbonate............	·045	nil
	99·245	99·50

SOILS OF THE LOWER GREENSAND.

The principal outcrops of the Lower Greensand in Cambridgeshire are:

(1) Around Aldreth and Haddenham.

(2) A narrow strip running from Lolworth through Oakington to Cottenham.

(3) At Gamlingay and extending through Potton and Sandy into Bedfordshire.

The weathered Greensand is red because of the oxidation of the ferrous iron in the original glauconitic grains, and it is characterised by the "box stones" and iron stones it contains. These are ferruginous concretions. Greensand gives rise to red soils which are liable to be severely scorched in summer.

Here the larger sized particles are very abundant, as much as from 60 to over 80 per cent. were stopped by a sieve with 100 meshes to the linear inch. The percentage of "clay" (which is of a totally

TABLE XX.

Mechanical Analyses of Lower Greensand soils.

	No. 5		No. 23		No. 18		No. 9		No. 16	
	Soil	Subsoil	Soil	Subsoil	Soil	Subsoil	Soil	Subsoil	Soil	Subsoil
Depth of sample in inches	6¼	6¼	7	6	6	6½	7	6½	5½	6
Stones, diameter over 3 mm.	per cent. 5·3	per cent. 4·2	per cent. 5·7	per cent. ·9	per cent. ·8	per cent. ·3	per cent. 6·1	per cent. 10·2	per cent. 2·7	per cent. 3·8
Fine Gravel	2·62	1·73	7·15	6·57	1·57	1·84	3·25	4·93	3·03	2·7
Coarse Sand	71·90	73·93	81·78	77·65	67·93	70·63	54·54	47·16	55·78	52·81
Fine Sand	4·62	5·08	3·37	6·14	7·35	6·36	9·92	8·22	11·14	8·54
Silt	4·23	4·37	1·80	1·33	4·49	3·92	8·81	9·87	8·05	7·86
Fine Silt	2·21	2·01	·81	1·01	3·89	2·89	4·15	4·66	4·20	4·43
Clay	7·20	6·74	2·63	3·57	7·67	11·10	7·88	18·39	12·06	17·16
Moisture	1·24	1·77	·57	·74	1·70	1·22	1·40	1·92	1·56	2·16
Loss on ignition (less CO_2)	5·58	3·99	2·47	2·16	4·58	3·16	5·94	7·02	5·20	4·86
Calcium Carbonate	nil	nil	nil	nil	·318	·038	nil	nil	nil	nil
	99·60	99·62	100·58	99·17	99·498	101·158	95·89	102·17	101·02	100·52

different nature from that of the heavy soils, being red in colour and nearly all ferric oxide) is sometimes higher than would be expected. A noteworthy feature is the total absence of calcium carbonate. The soils are very dependent upon the addition of humic matter to increase their water-holding capacity. Those found in the Gamlingay and Potton district are coarser grained than those from the Lolworth and Oakington Greensand. In the latter some of the "clay" has been washed through into the subsoil, forming a hard pan when dry. Most of the samples were found to be acid in reaction. The soils around Gamlingay and Potton grow market garden produce. They are heavily manured with London dung and respond to liberal treatment. The soils near Lolworth and Oakington which contain a higher percentage of clay are naturally superior to those of Gamlingay. All the Greensand soils are easy to work, the great difficulty of the farmer being lack of moisture, but the liberal use of London dung or farmyard manure greatly increases their water-holding power.

TABLE XXI.

Chemical Composition of Greensand soils.

	No. 5	No. 23	No. 18	No. 9	No. 16
Moisture	1·77	·57	1·70	1·40	1·56
Organic Matter, etc.	5·58	2·47	4·58	5·94	5·20
Insoluble Siliceous Matter	82·03	91·22	85·13	80·94	80·97
Lime (CaO)	·065	·085	·34	·26	·15
Magnesia (MgO)	·08	·125	·24	·17	·14
Phosphoric Acid (P_2O_5)	·204	·259	·197	·169	·146
Potash (K_2O)	·236	·278	·47	·443	·47

It will be seen that these correspond very closely, revealing a fairly high content of phosphate, little potash, and very little magnesia and total lime.

The quality and cropping powers of these soils may be inferred from the following particulars.

TABLE XXII.

Crops grown on the Greensand.

No. 5	No. 23	No. 18	No. 9	No. 16
Fairly elevated situation. 1901 Potatoes, fair crop 1902 Oats ,, ,, 1903 Potatoes ,, ,, 1904 ,, ,, ,, Scorching in summer a difficulty.	Elevated situation and very liable to scorching. Land had been barren for 20 years, then— 1902 Potatoes, very bad crop 1903 Rye, 20 bus. per acre 1904 Peas, 12 bus. per acre 20 tons dung per acre used for Peas.	Very good soil. 1902 Clover, 1½ tons hay per acre 1903 Wheat 32 bus. per acre 1904 Swedes, a little finger and toe in patches 1905 Barley Soil suited to a damp season.	A very fertile field. 1902 Clover, 1½ tons hay 1st crop, 1 ton hay 2nd crop 1903 Barley, averaged 40 bus. per acre 1904 Barley, averaged 40 bus. per acre	Good soil. 1902 Wheat, 28 per acre 1903 Swedes, crop fed o sheep 1904 Barley, 24 per acre because o weather 1905 White Clov Beans used a alternative to c because of cl sickness.

TABLE XXIII.

Weeds of the Greensand.

Specific name	Common name	Remarks
Stellaria media	Chickweed	Very large quantities
Chenopodium album	Fat hen	Large quantities
Polygonum aviculare	Knot grass	,, ,,
Capsella bursa pastoris	Shepherd's purse	,, ,,
Senecio vulgaris	Groundsel	,, ,,
Spergula arvensis	Field Spurrey	,, ,,
Rumex acetosa	Sorrel	,, ,,
Lychnis vespertina	Campion	,, ,,
Papaver Rhoeas	Poppy	,, ,,
Veronica agrestis	Speedwell	,, ,,
Crysanthemum segetum	Wild Marigold	Especially where acid
Viola tricolor	Field pansy	Large quantities
Plantago lanceolata	Plantain	Fairly numerous
Anthemis Cotula	Stinking Mayweed	,, ,,
Sherardia arvensis	Field Madder	,, ,,
Daucus carota	Wild Carrot	,, ,,

On No. 16, Crysanthemum segetum and sorrel grew almost exclusively on those patches where "Finger and Toe" attacked the swede crop. This was also the case on soil No. 9.

THE HYBRIDISATION OF BARLEYS.

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THE following experiments on the hybridisation of barley were commenced in 1901; consequently the inheritance of some of the characteristics has been known for some time. In view of the fact that from the earlier accounts of Rimpau and Tschermak the main outlines of the story could be traced without any special difficulty, there appeared to be no necessity for immediate publication. This was delayed, therefore, in order to complete the investigation of one or two doubtful points. The literature of barley-breeding published prior to the year 1900 is rather extensive, but of comparatively little interest to the modern student of heredity. The most important papers are those of Liebscher[1] and Rimpau[2]. That part of Rimpau's great paper, "Kreuzungprodukte Landwirtschaftliche Kulturpflanzen," dealing with barley, is of exceptional interest on account of its extreme thoroughness and the completeness of the records it contains. As one reads it one cannot help thinking that Rimpau must have come very near to making an independent discovery of Mendel's laws of inheritance.

The details of the cross between Steudelgerste and Gabelgerste will serve to illustrate this point. In these varieties the following characters are represented, four and two rows of grain, awned and trifurcate paleae, black and white colour and naked and covered grain. Rimpau raised a large number of plants from the grain of the hybrids and found that they could be grouped into a series consisting of sixteen distinct types as follows: four or two row barleys with normal or trifurcate awns: black and white forms of each of these four types

[1] Liebscher, *Bot. Centrb.* Vol. XL. p. 232 (abstract).

[2] Rimpau, *Landw. Jahrb.* Vol. XX. p. 354. See also Wittmack, *Ber. d. deut. Bot. Ges.* IV. p. 434.

which finally had either naked or enclosed grain. These are the sixteen types expected on the assumption that the characters present in the parents are capable of independent segregation. Rimpau raised three further generations of all of these types, but evidently sowed grain from a number of individuals of each. Their behaviour is tabulated in some detail. One or two anomalous cases occur in the descriptions which are probably due more to self-sown grain than actual errors, but on the whole the analysis of their behaviour agrees well with the results expected from the Mendelian standpoint. Other cases are examined in the same fashion, but apparently on a less extensive scale, and these also show the same general correspondence with the expectations we should form to-day.

In the following experiments some of the types resulting from Rimpau's crosses have been used as parents together with many other varieties. For the majority of these I am indebted to Mr E. S. Beaven of Warminster, who kindly presented a large collection to the Cambridge Agricultural Department.

The numerous varieties of barley in existence provide a large number of differentiating characteristics. These are described below at some length because many are wanting in our cultivated types which form a very small proportion of those known, but not cultivated on an extensive scale.

The distinguishing characteristic of the genus Hordeum is that the one-flowered spikelets are arranged in groups of three alternately on the rachis. Each of the spikelets has a pair of glumes at its base. The cultivated barleys are grouped together as a single species *Hordeum sativum* (Pers.) divided into a number of sub-species. These probably represent elementary species as defined by de Vries. As in most large groups of closely related forms the classification is often a matter of considerable difficulty. Perhaps the most convenient scheme is that of Körnicke as modified by Beaven[1]. In this the following sub-species are recognised:—*H. hexastichum, H. vulgare, H. intermedium, H. distichum, H. zeocriton,* and *H. decipiens.*

H. hexastichum is sometimes grown in this country for forage, and is then winter sown. It is commonly found in commercial samples of Persian, Chilian, and Beyrout barleys. In this group all of the spikelets are fertile and the internodes are short. It is therefore known popularly as six row barley with dense or wide ears.

[1] Beaven, *Journ. Inst. of Brewing*, Vol. VIII. p. 542.

H. vulgare is commonly known as "bere" or as four rowed barley. Körnicke names the group *H. tetrastichum* on this account. In reality the barley is six rowed, so that the term is deceptive. Its use appears to be responsible for the idea that in this type the median floret of the group of three has been suppressed, leaving only pairs of lateral florets on either side of the rachis. It differs from *H. hexastichum* in having long internodes so that the ears are lax or narrow. The lateral florets of alternate groups partially overlap one another, and consequently the six rows are not so clearly marked as they are in *H. hexastichum*, and the ear appears to be more or less four-sided. Varieties of *H. vulgare* are largely imported into this country from California, the Argentine, Smyrna, and the Black Sea districts. "Bere" is also cultivated to a certain extent.

H. intermedium is a group consisting of at present only two varieties of no importance from the technical point of view, but of some interest to the biologist. The lateral florets in these are small and awnless, but as a rule they set grain. One of the varieties was found by Haxton in a field of bere, and he described it as a transition form between bere and the normal two rowed barley[1]. In my cultures many of the lateral florets are frequently sterile.

H. distichum has a fertile median floret and sterile laterals in each group of three spikelets. The lateral florets are staminate and reduced in size. The internodes are long, and consequently the ears are described technically as narrow and two rowed. The group is represented in this country by the Chevallier and Archer barleys.

H. zeocriton is characterised by staminate lateral and fertile median florets and a dense or wide ear. *H. distichum* and *H. zeocriton* are thus parallel groups to *H. vulgare* and *H. hexastichum*. The various Goldthorpes represent this group in this country.

H. decipiens has the lateral florets still further reduced. Its varieties show mere traces of these structures with a pair of glumes at the base. No sexual organs are present in these rudimentary spikelets. The median florets are fertile. The group is cultivated in Abyssinia, but it is little known here and never cultivated as a crop. At present the lax-eared varieties are fairly numerous and the wide-eared so rare that no group parallel with *H. zeocriton* has been made to receive them. As will appear later there is no difficulty in raising such forms.

[1] Morton's *Cyclopaedia of Agriculture*, 1869, p. 183.

Besides the characters afforded by the fertility or otherwise of the spikelets and the internode length, there are many others. The paleae provide some of considerable importance. In most barleys the paleae are prolonged to form long, serrated awns, the ear being then known as bearded. In some few varieties the awns are smooth, whilst in others they are wanting, the variety being then beardless. Such forms must not be confused with the so-called beardless barleys which shed their awns on ripening. The paleae may also be "trifurcate" as in the case of Nepaul barley. The term is used to describe a small hood-like swelling either at the apex of the paleae or borne on a short awn. At the base of this hood (kapuzen) are a pair of pointed auricle-like processes, and within the structure itself there is a rudimentary flower which may at times set grain. If the palea may be considered to be a modified leaf sheath, the auricles correspond with those of the leaf and the flower is epiphyllous, being borne on the leaf blade[1].

The colour of the paleae of different varieties of barleys is often very characteristic. In our cultivated forms it is yellow or yellowish grey as in the Archer barley. Black and purple paleae are however common. As a rule this purple colour is most marked before the grain is ripe. The extent to which it persists appears to depend on the weather conditions, but even when it is faded some traces usually remain which enable one to say whether the paleae were purple or not. The black colour also develops as the ears ripen, but it is persistent.

These coloured paleae are generally associated with coloured grain, black or purple eared barleys generally having grain varying in colour through shades of violet, brown-violet or green-violet. It appears that these colours in the paleae are associated with those of the grain. In addition to colour characteristics the grain provides others. The shapes differ to a certain extent, but little attention has been paid to this at present, and the caryopsis may, or may not, be fused with the paleae; in the latter case the grain is described as naked, in the former, for the sake of convenience, I have called it "trapped."

The glumes in the majority of the barleys are small and not conspicuous, but in some few varieties they are ovate lanceolate in shape and occasionally more or less awned. The rachilla provides a useful pair of characters to those who handle barleys commercially. It may be long and almost hairless, or it may be short and covered with silky hairs. The former condition is known as "smooth," the latter

[1] Cf. Raciborski, *Bot. Centrb.* Vol. xc. p. 407 (abstract).

as "bristly." Other characters of less importance will be referred to later.

The operation of crossing barleys is not particularly difficult, but it cannot be carried out as rapidly as in the case of wheat. After various trials the following method was adopted. The sheath was split open when the awns were emerging and the ear freed from it. All except from eight to twelve median florets were stripped from the rachis, and these were then emasculated. The simplest method for removing the stamens is to cut off the apex of the paleae. The proper height to make the cut can as a rule be determined by holding the ear up to the light, when the position of the stamens can be detected. Through the opening so made into the flower, the stamens can be removed without tearing the paleae. Attempts to open the paleae to remove the stamens so often resulted in failure that this method was abandoned towards the end of the experiments. To pollinate the stigmas, stamens just at the stage of breaking were inserted into the opening at the apex of the paleae. These were obtained as in the case of wheat, by making use of the peculiar elongation of the filaments when the stamens are ready to dehisce. The tips of the florets of ears of the variety required as the male parent were cut off and laid aside for a few minutes when, if sufficiently ripe, the stamens protruded and could readily be removed. After pollination the ears were enclosed in small bags of thin paper water-proofed by soaking in paraffin wax. These were generally allowed to remain on the ears until harvest. As in the case of wheat pollination rarely failed in fine weather, but when wet, failure was the general rule.

The arrangement of the plots and the records was the same as that described in the wheat-breeding experiments.

Brief descriptions of the varieties used as parents are appended as these are little known to those who have not given special attention to this group of plants[1].

H. hexastichum.

H. pyramidatum (Kcke.). Ears dense, pyramidal. Paleae awned and white.

H. Schimperianum (Kcke.). Ears dense, black, awned paleae enclosing the grain which is black also, rachilla bristly.

[1] Detailed descriptions will be found in Körnicke and Werner in Bde. I. and II. of their *Handbuch des Getreidebaues*, Berlin, 1885, or in Körnicke, *Die Hauptsachlichsten Formen der Saatgerste*, Bonn, 1895.

H. japonicum. Ears dense, paleae yellow, with broad awns, grain naked white.

H. densifurcatum. Ears dense and six rowed, paleae black and trifurcate, glumes lanceolate.

H. eurylepis (Kcke.). Ears dense, glumes ovate-lanceolate and awned.

H. hexasticofurcatum (K. H.). Paleae trifurcate, white, enclosing the grain.

H. vulgare.

H. vulgare (L.), *H. pallidum* (Ser.). Ears lax, paleae awned, yellow, enclosing the grain which is light in colour.

H. himalayense (Rittig.). Ears lax, paleae grey or yellow, grain naked and violet.

H. trifurcatum (Schl.). Known as Nepaul barley or sometimes as Nepaul wheat. This variety is the "dreigablige gerste" of German writers. Ears less lax than in most varieties of the group *H. vulgare.* Paleae ending in hood-like expansions containing supernumerary florets (trifurcate paleae), grain naked.

H. aethiops (Kcke.). Ears narrow, six rowed, paleae black, trifurcate, grain naked, black.

H. atrum (Kcke.). Ears lax, six rowed, paleae and grain black, trifurcate.

H. violaceum (Kcke.). Ears lax, paleae awned, purple when unripe, changing to dull yellow or grey as a rule when ripe, but in some seasons retaining a purple tinge. Grain naked, purple to greenish violet in colour.

H. intermedium.

H. transiens (Kcke.). Ears dense, lateral florets small but fertile and awnless.

H. Haxtoni[1] (Kcke.). Median florets fertile and awned, lateral florets small but fertile, awnless.

H. distichum.

H. nutans (Schubl.). Chevallier barley. Ears lax, paleae awned, white, enclosing the grain, rachilla smooth.

H. rigens (K. H.). Similar to Chevallier, but with awns which are smooth from below.

[1] Morton's *Cyclopaedia of Agriculture*, 1869, p. 183.

H. inerme (Kcke.). Ears lax, paleae awnless, white. One of the few varieties of barley in which the awn is wanting. It originated from a cross of Rimpau's between *H. Steudelii* and *H. trifurcatum*.

H. nigrosubinerme (Kcke.). Paleae practically awnless, black.

H. ianthinum (Kcke.). Ears lax, paleae blackish, awned, grain naked and violet.

H. utriculatum (K. H.). Ears lax, paleae light in colour, trifurcate, the hoods unusually large and sessile. Grain naked. The supernumerary flowers are occasionally fertile.

H. nigrescens (Kcke.). Ears narrow, two rowed, paleae blackish, awned.

H. spontaneum (C. Koch). Ears two rowed, paleae with harsh thick awns, grain narrow, enclosed by the paleae, rachis brittle. The variety is a native of Persia, Palestine and other parts of Asia, and it is supposed to be one of the wild prototypes of the modern barleys. In this district it is perfectly hardy, and owing to its habit of shattering when ripe, becomes a weed unless it is harvested early. In the seedling stage it is easily recognised by its strongly twisted foliage which lies on the soil weeks after most varieties have become upright. A more detailed description will be found in Körnicke.

H. zeocriton.

H. zeocrithum[1] (L.). Goldthorpe type. Ears dense, paleae awned, white, enclosing the grain, rachilla bristly.

H. decipiens.

H. deficiens (Steudel). The variety is typical of the group *H. decipiens*. Spike lax, narrow and, partly owing to the entire suppression of the lateral florets, peculiarly slender. Paleae awned, bright yellow, enclosing the grain. The paleae open more at the flowering period than most barleys, but the variety appears to be truly autogamous.

H. Steudelii (Kcke.). Very similar to *H. deficiens* in shape, but the paleae and the grains are black.

H. Abyssinicum (Ser.). Ears lax, paleae awned, almost white in colour, enclosing the grain, glumes lanceolate and shortly awned.

H. decorticatum (Kcke.). A variety of *H. decipiens* with black paleae and grain; paleae non-adherent to the grain.

[1] Linnaeus, *Species Plantarum* (1753), p. 85.

F. 1 *Generation.*

H. Schimperianum × *H. nutans.* Ear lax but slightly denser than a normal Chevallier, two rowed, paleae and grain black, rachilla bristly, glumes with slight awns.

H. pyramidatum × *H. deficiens.* Ears lax, resembling those of a Chevallier barley, slightly denser than those of the male parent, glumes with short awns.

H. japonicum × *H. Steudelii.* Ears lax and Chevallier-like, with larger lateral florets than those of *H. Steudelii,* paleae black with ribbon-like awns, grain for the most part trapped, violet-black in colour, glumes with small awns.

H. vulgare × *H. Steudelii.* Ears lax, Chevallier-like, paleae black and awned, grain trapped, black.

H. trifurcatum × *H. nutans.* One plant only was secured and this was attacked by Helminthosporium and failed to set any grain. Ears of the Chevallier type, but a little denser, paleae with awns from three to nine cms. in length bearing hoods for the most part, about half-way up, but in some cases terminally.

H. transiens × *H. deficiens.* Ears laxer than those of *H. transiens* but denser than those of *H. deficiens,* lateral florets not as large as those of *H. transiens,* and containing stamens only, glumes with short awns.

H. inerme × *H. Haxtoni.* Ears of the Chevallier type, awnless.

H. nutans × *H. himalayense.* Ears lax, paleae greyish yellow, grain naked and violet. Many of the lateral florets on each of the plants were fertile. Grain not truly naked; on rubbing out an ear some grains escaped from the paleae, but the majority remained enclosed, violet, rachis brittle when ripe.

H. nutans × *H. Steudelii.* Ears lax, lateral florets minute but better developed than those of the male parent, paleae of the median florets black, of the minute laterals white. Grain black.

H. ianthinum × *H. utriculatum.* Ears of the Chevallier form; paleae tinged with violet, trifurcate, the supernumerary florets exceptionally large and occasionally fertile, sessile, grain naked and purple.

H. nigrescens × *H. aethiops.* Ears of the Chevallier type, but with somewhat larger lateral florets which occasionally set grain, paleae black with supernumerary florets on short stalks up to two cms. in length.

H. rigens × *H. atrum.* Ears of the Chevallier type, but in two plants out of a total of eight some of the ears had fertile lateral florets here and there. Paleae black with hoods on stalks some two cms. in length. Grain when divested of the adherent paleae purple.

H. spontaneum × *H. eurylepis.* Ears two rowed, glumes narrow, awned, grain narrow, rachis brittle. At first sight the hybrid seemed identical with *H. spontaneum*, but closer inspection showed the greater development of the awns.

H. spontaneum × *H. hexasticofurcatum.* Ears lax and two rowed. Paleae ending in an awn about two cms. in length bearing a terminal hood and secondary floret, lateral florets larger than those of *H. spontaneum* but not fertile, grain trapped and slender, rachis brittle. The spikes scattered as soon as ripe, but owing to the lack of awns the grains were unable to bury themselves so effectively as those of *H. spontaneum.*

H. zeocriton × *H. nutans.* Ear lax, but less so than a normal Chevallier, nodding, rachilla bristly.

H. nigrosubinerme × *H. hexasticofurcatum.* Ears lax and of the Chevallier type, but with a fertile lateral floret here and there. Paleae black and awnless.

H. deficiens × *H. japonicum.* Ears of the Chevallier type, less dense than those of the male parent, but denser than those of *H. deficiens.* Paleae with broad awns, more or less free from the grain. Grain more elongated than that of *H. japonicum.*

H. deficiens × *H. pyramidatum.* Ears Chevallier-like.

H. deficiens × *H. nutans.* Ears lax, lateral florets minute, but larger than those of the male parent, sexless.

H. deficiens × *H. violaceum.* Ears lax, resembling those of a Chevallier barley, purple when ripening, brown when ripe. Grain trapped, when stripped of the paleae deep violet in colour.

H. deficiens × *H. parallelum.* Ears similar to those of a Chevallier barley, but the laterals a little smaller, glumes with short awns.

H. Abyssinicum × *H. Steudelii.* A typical *decipiens* with black paleae and grain with narrow glumes.

H. Abyssinicum × *H. trifurcatum.* Ears lax, two rowed with the lateral florets similar to those of a Chevallier barley. Paleae white, ending in awns from one to four inches in length which bore either terminally or half-way along their length supernumerary florets. These varied considerably in their development, some contained perfect stamens and ovaries, whilst others were rudimentary with mere traces

of sexual organs. In extreme cases the florets were missing, the awn then being sharply bent about half-way up in the position in which they would, presumably, have occurred. Grain enclosed by the paleae, glumes awned slightly.

H. decorticatum × *H. densifurcatum*. Ears lax and Chevallier-like; paleae black, bearing nearly sessile hoods, lateral florets lighter in colour than the median, grain slender, partially naked and black.

Sexless and Staminate Lateral Florets.

A few crosses have been made between a Chevallier barley (*H. nutans*) and two of the varieties of the sub-species *H. decipiens*, in which the lateral florets are so reduced that it is difficult to distinguish even the paleae as such. These lateral florets are entirely destitute of sexual organs. The crosses were as follows:—

H. nutans × *Steudelii*.
H. Steudelii × *nutans*.
H. nutans × *deficiens*.

The hybrid in all cases bore sexless lateral florets, but the paleae were slightly more developed than in the corresponding parents. In those descended from the black-eared *H. Steudelii* these rudimentary lateral florets showed up like white stitches on a black ground. The F. 2 generation consisted of plants of three types bearing staminate, small or sexless lateral florets. The groups were perfectly distinct from one another, and could readily be sorted. The proportions for each plot were as follows:—

Staminate	Small	Sexless
41	62	20
39	78	36
54	119	56

Taken as a whole these results indicate that the types occur in the ratio of 1 : 2 : 1, though the first quoted is a rather wide departure from the normal. This is in all probability fortuitous, as the reciprocal cross obviously gives the 1 : 2 : 1 ratio. A number of the heterozygotes with the small lateral florets were dissected under a lens, but no stamens, fertile or otherwise, could be detected in any case. Thus the sexless condition might be described as dominant over the staminate if no attention were paid to the slight increase in development of the lateral florets of the heterozygote.

A few sowings of each of these three types have been made. Grains from plants with small lateral florets produced the three types

again in each of the 20 cases tested. A similar number of plants with staminate lateral florets proved to be homozygous, and 15 plants with the rudimentary lateral florets of the parents also bred true to this feature.

Hermaphrodite and Sexless Lateral Florets.

This pair of characters has been investigated in the following crosses :—

(*a*) *H. deficiens* × *violaceum.*
(*b*) *H. japonicum* × *Steudelii.*
(*c*) *H. vulgare* × *Steudelii.*
(*d*) *H. Abyssinicum* × *trifurcatum.*
(*e*) *H. pyramidatum* × *deficiens* and its reciprocal.
(*f*) *H. deficiens* × *parallelum.*
(*g*) *H. decorticatum* × *densifurcatum.*

The F. 1 plants bore small lateral florets which, when examined in 1903, (*a*—*d*) were considered to be sexless, as the stamens appeared to be rudimentary and incapable of producing normal pollen grains. This view was negatived in the following season when a further series of F. 1's was available for more detailed examination, as well as a series of F. 2's. These showed conclusively that the normal form of the heterozygote was characterised by the formation of truly staminate laterals. From the systematist's point of view it would be described as *H. distichum* or *zeocriton* according to the laxness or denseness of the ears.

In the F. 2 generation the fully fertile, the staminate, and the rudimentary lateral bearing types were met with in the proportions of 1 : 2 : 1. The actual figures given in the same order as the list above were :—

26 : 52 : 23, 16 : 47 : 21, 30 : 65 : 25, 39 : 85 : 44,
54 : 114 : 55, 80 : 147 : 74, 47 : 98 : 44.

The three groups were perfectly distinct from one another, and no forms occurred which could be described as doubtfully belonging to one group or another. A subsequent generation was raised from each type. In all, 48 cultures of forms with hermaphrodite lateral florets and 62 with rudimentary lateral florets were grown, and in every case, no matter what the parents, they bred true to these characters: 110 cultures of the heterozygote with staminate laterals were also raised, and these, without exception, produced the three types once more. Complete

statistics of these groups were not considered necessary, as from an inspection of the plots it was evident that the types again occurred in the ratio of 1 : 2 : 1. In one case, *H. pyramidatum* × *deficiens*, an F. 4 generation containing several hundred plants was grown, all of which proved true to the original six row type sown. In addition to the series already described, a cross was made between *H. transiens* with small, but hermaphrodite, lateral florets and *H. deficiens*. The F. 1 again produced staminate lateral florets. Only one poor plant was raised, and this gave in the next generation seven plants with small, but fertile lateral florets, 13 with staminate, and 15 with rudimentary lateral florets. The numbers are too small to lay much stress upon, and in all probability the somewhat large departure from the general ratio is due to the smallness of the count. All of the forms with staminate laterals were sown, and they in turn split off the forms with hermaphrodite and rudimentary lateral florets.

Staminate × Hermaphrodite Lateral Florets.

The varieties with staminate lateral florets include the Chevallier and Goldthorpe types, that is the so-called two rowed barleys, whilst those with hermaphrodite lateral florets include the six row and the so-called four rowed barleys. As these are the types in general cultivation, there are naturally a considerable number of crosses between them recorded in the earlier literature of the subject, nevertheless it is difficult to determine the behaviour of these characteristics from the descriptions given. Rimpau's[1] account of a cross between Pfauengerste and Gabelgerste (Fan or Peacock and Nepaul barley) is perhaps one of the most satisfactory of these. He describes and figures the F. 1 as being intermediate between a two row and a four row barley, the lateral florets being partly fertile. These florets, further, were hoodless, whilst those occupying the middle position of the group of three were hooded. In a natural cross between *H. pallidum* and *H. nutans* he again observed this same form in the heterozygote. Tschermak[2] found that the two row condition was dominant over the four and six row in the F. 1, but in the generation raised from it the splitting was impure. Wilson[3] in the case of Standwell and Bere found evidence that "seemed to warrant the assumption that the two row character was recessive," but in the succeeding generation the form of the individuals appears to have been

[1] Rimpau, *Landw. Jahrb.* Bd. xx. p. 356.

[2] Tschermak, *Deutsche Landw. Presse*, xxx. Nr. 82.

[3] Wilson, *Journ. Agric. Sci.* Vol. II. p. 86.

more or less indeterminate. In a second example where Standwell was crossed with a six row barley, the six row character was recessive.

In a former paper dealing with this subject I have described a series of F. 1 plants and one F. 2 generation, which indicated that the two row type was dominant over the six row. As will be shown later this view is not altogether correct.

These characters have been investigated in the following series of crosses:—

H. Schimperianum × *nutans.*

H. nigrosubinerme × *hexasticofurcatum* and its reciprocal.

H. spontaneum × *hexasticofurcatum.*

H. trifurcatum × *nutans.*

H. spontaneum × *eurylepis.*

H. rigens × *atrum.*

H. nutans × *himalayense.*

H. nigrescens × *aethiops.*

H. persicum × *elongatum.*

The F. 1 generation of the first five examples was grown in 1904, and all of the plants appeared to possess the ordinary staminate lateral florets of the two rowed parent, for no grain was set in any case. The six rowed type was thus recessive to the two rowed, and this view was borne out by the fact that an F. 2 generation of the cross between *H. hexastichum* × *nutans* consisted of two row and six row forms in the ratio of 3 : 1. In the remaining four examples the F. 1 grown in the following year was, from the morphological point of view, a form of *H. intermedium,* inasmuch as the lateral florets were fertile, smaller than the median florets and destitute of awns or hoods. Among the F. 2's of the previous series were many examples with similarly developed ears.

The F. 2 of *H. Schimperianum* × *nutans* was chosen for a detailed examination of the degree of fertility of the lateral florets. It was found to contain 49 individuals with the large fertile lateral florets, and 46 with the small staminate lateral florets characteristic of the two parents. Of the remaining 99 individuals, 16 belonged to the group *H. intermedium,* and 83 bore either a few fertile, and small, lateral florets or florets which were larger and more pointed than those of the parent with the staminate lateral florets. Sowings were made of each of the *H. intermedium* types, and also of 20 individuals showing varying degrees of development of the lateral florets. In some of these a few lateral florets were fertile, but the majority were grainless. The whole series

proved to be heterozygotes, each sowing giving the three expected types. The totals for the whole series were 103 with fully fertile, 211 with small but more or less fertile, and 98 with staminate lateral florets similar to those of the parent *H. nutans*. No differences were detected in the progeny from ears in which all the small lateral florets were fertile, and those in which no grain was set. From this there can be no doubt that the F. 2 generation consisted of six row, intermediate and two row forms in the proportion of 49 : 99 : 46, or in the ratio of 1 : 2 : 1.

In the subsequent examination of such forms those individuals with enlarged lateral florets have always been considered as heterozygotes. Thus in *H. nutans* × *himalayense* the F. 2 consisted of 40 plants with large fertile laterals, 80 with smaller and intermediate, and 41 with staminate lateral florets. Similar indications of this 1 : 2 : 1 ratio have been observed in the other crosses, but they still have to be examined statistically[1].

A considerable number of the typical six row and two row forms from the first five crosses have been tested in the F. 3. In all the trials amount to 85, and in each case the individuals tested have proved to be homozygous.

The heterozygote therefore of forms with hermaphrodite and staminate lateral florets is potentially hermaphrodite, and of the type known to systematists as *H. intermedium*. As a general rule the small lateral florets are hoodless and awnless, though in some cases traces of these structures have been observed, more particularly in a cross between *H. rigens* and *atrum*.

Investigations on the anomalous results of the F. 1 generation grown in 1904, are still being carried out. As far as the tests have gone at present, the incomplete development of the lateral florets appears to have been due to external conditions. Owing to a shortage of space the grains were planted rather closely together and somewhat late in the season. In the following year when the hybrids were typical *H. intermedium* forms, the grains were planted at six inch intervals in rows a foot apart, and, as many failed to germinate, the plants had every opportunity for vigorous development. That the space at the disposal of the plant largely determines the degree of development of the lateral florets of the heterozygote is also indicated by the fact that when F. 2's are standing thinly in the plots, there is not such a large number

[1] The most aberrant result met with so far is in the case of *H. nigrescens* × *aethiops* where the proportions are 24 : 65 : 26.

of individuals with poorly developed lateral florets as in the case described in detail above.

One cross has been made to determine the results of crossing *H. intermedium* with a variety with staminate lateral florets. The parents in this case were *H. transiens* and *H. inerme*. The F. 1 bore staminate lateral florets. The F. 2 consisted of individuals with lateral florets similar to those of the parents and in addition of true six row barleys. The result was found to be due to the fact that the *H. inerme* used as a parent was in itself a heterozygote, for it was throwing six rowed barleys as well as the type. The number of individuals raised in the F. 2 was too small to attempt to unravel this complication, and the experiment was temporarily abandoned.

"Hooded" or Trifurcate and Awned Paleae.

Examples of parents carrying one or the other of these characters are provided by the following crosses:—

(*a*) *H. Abyssinicum* × *trifurcatum.*
(*b*) *H. spontaneum* × *hexasticofurcatum.*
(*c*) *H. trifurcatum* × *nutans.*
(*d*) *H. decorticatum* × *densifurcatum.*
(*e*) *H. ianthinum* × *utriculatum.*
(*f*) *H. rigens* × *atrum.*
(*g*) *H. nigrescens* × *aethiops.*

The F. 1 was in all cases hooded, the supernumerary florets being almost sessile in *b*, *d*, *e*, *f* and *g*, whilst in *a* and *c* they were borne on awns from half to four inches in length. The length of the awn varied considerably on one and the same ear.

The development of the supernumerary florets when borne on the awns was not so complete as in the parents, and frequently one was missing here and there in an ear, its position being then marked by a kink in the awn.

In the F. 2 generation hooded and awned forms were produced in approximately the ratio of 3 : 1. Thus the series taken in order gave the following figures:—113 : 43, 57 : 30, the F. 1 plant of *c* died before maturing any grain, 143 : 46, 91 : 29, 201 : 65, 96 : 37, or a total of 701 : 250 equivalent to the ratio of 2·8 : 1.

In the F. 2 generation of *a* and *c* there was considerable variation in the length of the awns carrying the supernumerary flowers, but no indications could be detected of segregation into individuals with

sessile hoods, awned hoods, and true awns only. In the case of the cross between *H. Abyssinicum* and *H. trifurcatum*, no plants with hoods as sessile as those of the parent were found in either the F. 2 or F. 3 generation. Further no plants with hermaphrodite lateral florets bore awns except on the median florets. Such individuals from a systematic point of view would be classed in the group *H. intermedium*. In the parent the fertile lateral florets are smaller than is generally the case with forms of *H. vulgare*, and the hoods of these florets are rudimentary or wanting, so that it is possible that the proper position of *H. trifurcatum* is in the group *H. intermedium*, of which at present it would form the only hooded representative. Unfortunately the only other cross with this variety as a parent died in the first generation, so that no other data are for the time being obtainable. Where the hoods of the lateral florets are well developed as in *H. hexasticofurcatum*, *atrum* or *aethiops*, the corresponding fully awned florets were met with in all cases.

In the F. 3 generation the 45 awned types of various descent tested were found to breed true to this character, whilst of the same number of hooded types, 16 were pure, and 29 gave a mixture of hooded and awned individuals. Six individuals with hoods borne on awns of two or more inches in length from *H. Abyssinicum* × *trifurcatum* which were tested, all bred true to this character, though in three of the cases they split into six row and two row types. The permanence of this feature suggestive of a blend of the parent characteristics was not expected, and no explanations can yet be offered to account for it.

Black and White Colour in the Paleae.

The fact that the black colour is dominant over white is evident from many pre-Mendelian crosses. Cases are described for instance, by Rimpau[1], in which the hybrid was black, and black and white forms appeared in the progeny. More recently Tschermak[2] has investigated the inheritance of these characters, and shown that the black and white forms occur in the ratio of 3 : 1 in the F. 2. The following crosses are between black and white varieties:—

H. japonicum × *Steudelii.*
H. vulgare × *Steudelii.*
H. Abyssinicum × *Steudelii.*

[1] Rimpau, *ibid.*
[2] Tschermak, *ibid.*

H. Schimperianum × *nutans*.
H. nigrosubinerme × *hexasticofurcatum*.
H. nutans × *Steudelii*.
H. rigens × *atrum*.
H. persicum × *elongatum*.

In each case the heterozygote was as black as the black parent, and in the F. 2 the expected black and white forms appeared in the ratio of 3 : 1. The figures obtained were as follows:—68 : 24, 95 : 25, 32 : 8, 154 : 55, 29 : 8, 94 : 29. Statistics for the last two crosses have not been obtained. Some 89 cultures of extracted whites have been grown without a single black-eared individual being produced, and in one case such a white form has been used for further crossing with white without producing any tinted individuals. The black forms proved to be pure with regard to this character or else heterozygotes. Twenty-four of the former class were obtained in a trial sowing of 75 extracted blacks.

Where the variety *H. Steudelii* was used as a black parent, it is worth noticing that the sexless lateral florets, produced when the second parent was *H. nutans*, or the staminate laterals when *H. vulgare* was the parent, were in all cases white. This same feature appeared in the heterozygotes of the two following generations. Up to the present white lateral florets on otherwise black ears have not been obtained in these experiments as stable forms, but they exist as such in such varieties as *H. pictum*.

Purple and White Paleae.

In several varieties of barley the paleae, before the grain begins to ripen, is a vivid purple colour. As ripening progresses this colour disappears, and by the time the crop is ready for harvesting the paleae are a dingy grey colour, showing, however, some signs of its original purple colour. It is advisable therefore to determine this feature in the crop at an early stage.

The crosses made to determine the inheritance of this purple colour were between *H. deficiens* and *H. violaceum* and *H. ianthinum* and *H. utriculatum*.

In each case the F. 1 was as purple as the purple parent, and its descendants consisted of individuals with purple or white paleae. In the first case the ratio of purple to white was 70 : 28, in the second, 91 : 29.

An F. 3 generation of the first cross only has been raised. Twelve white individuals produced only white offspring, whilst three out of 12 purples were pure, and the remaining nine threw purples and whites. No indications of intermediate shades between these two were met with in any case, so that purple may be described as simply dominant over white.

Colour of Grain.

Black colouring in the paleae appears to be associated with colour in the grain. Up to the present no cases have been met with amongst the hybrids in which light grain occurs on plants with dark paleae or dark grain on plants with light paleae[1]. In wheats, on the contrary, colour (red) in the grain is independent of the coloured or colourless condition of the glumes.

Under these circumstances coloured grain is dominant over colourless. It is doubtful whether this provides a complete expression for the facts observed, inasmuch as the colouring is very variable in the F. 2 generation. Thus ears with black paleae may contain grain in which the colour of the caryopsis is black, purple, or violet-green. The latter shades may be very faint, and then they are difficult to distinguish with certainty from the colourless grains. If, however, all grains showing any colour are classed as dark, those without as light, fair approximations to the 3 : 1 ratio are obtained. Further, plants producing colourless grains have invariably bred true to this character.

Narrow and Broad Glumes.

In the majority of the barley varieties the glumes are narrow, but some few have ovate-lanceolate glumes. These characteristics have been investigated in :—

H. Abyssinicum × *Steudelii* and *H. Abyssinicum* × *trifurcatum*.

The glumes of the F. 1 were in both cases narrow, and in the F. 2 narrow and broad glumes appeared in the approximate ratio of 3 : 1. In the first case the figures obtained were 29 : 11, in the second, 127 : 45. A few F. 3 cultures were raised from the latter cross with the result that all the broad glumed forms bred true to this character, whilst three out of eight of the narrow glumed forms proved to be pure.

[1] In *H. himalayense* coloured grain is found in conjunction with white or greyish-white paleae.

Lax and Dense Ears.

As far as one can determine from the existing records of barley hybrids, lax ears are dominant over dense. Judging from the general appearance of the hybrids raised in the course of these experiments, this would also be the case. But as in wheats this does not give a complete account of the phenomena observed in the F. 2 generation. Where extremely lax and dense ears are crossed in wheat then, as Spillmann was the first to demonstrate, the heterozygote is intermediate in this respect. Where the difference is less pronounced this cannot be traced with any certainty: in fact, cases have been recorded where the F. 1 is laxer than the lax parent, and the F. 2 has contained similar excessively lax forms. In such cases it may be that that laxness and denseness are dependent on more than one pair of characters.

Varying degrees of laxness and denseness of the ears are shown in most of the hybrids already described, but the most suitable cases for examination are provided in the following :—

H. zeocriton × *nutans.*

H. pyramidatum × *deficiens* and its reciprocal.

H. parallelum × *deficiens.*

In each case the F. 1 appeared to be as lax as the lax parent, though subsequent measurements have shown that it is slightly denser. The figures are derived from too small a series of plants to lay any stress on. This is due to the fact that a cross has to be made each time to secure a single plant, and the flowering period is so short that it is a matter of some difficulty to make all the necessary crosses. The F. 2 generation has consisted in each case of plants with ears as lax or as dense as those of the parents, together with a series lying between these extremes, which cannot be satisfactorily classified. Trial sowings of the extremes show that they are homozygous, but the heterozygotes cannot be distinguished with any degree of certainty by inspection only. In order to unravel the story, measurements of a series of F. 2 plants have been made, and the average internode length determined by dividing the length of the rachis by the number of the spikelets borne on it.

The figures for *zeocriton* × *nutans* are :—

mms.	1·6	1·8	2·0	2·2	2·4	2·6	2·8	3·0	3·2	3·4	3·6	3·8	4·0	4·2
individuals	0	2	15	24	17	7	26	44	39	23	8	2	2	0

for *H. pyramidatum* × *deficiens* :—

	3	7	14	19	12	42	41	28	15	6	4	2	2	1

H. Schimperianum × *nutans* :—

	0	0	2	7	13	30	24	19	14	18	4	5	0	2

The six row and the two row plants show the same distribution of lax and dense ears, the curves, if plotted separately, being the same in both. The first example quoted is perhaps the simplest. In this there are two groups of plants centred about an internode length of 2·2 and 3·0 mms. respectively. Unfortunately there appears to be no method of analysing such a curve without sowing all the individuals represented in it.

This test has been partially made. All the individuals with internode lengths ranging from 1·8 to 2·6 mms. were planted separately. Two with an average internode length of 1·8 bred true, and 15 of 2·0 mms. also bred true; of 24 of 2·2 mms. 20 were homozygous; of 17 of 2·4 mms. 15 were homozygous; of 7 of 2·6 mms. 4 proved heterozygotes. The pure dense forms thus fall into a series with internode lengths as follows:—

mms.	1·6	1·8	2·0	2·2	2·4	2·6
No. of plants	0	2	15	20	15	3

giving, considering the numbers in question, a singularly uniform Quetelet curve. The total number of dense-eared individuals was thus 55 in a generation consisting of 209, or a sufficiently close approximation to the 1 : 3 ratio.

No analysis of the group centering around 3·0 mms. has yet been attempted. Judging from the uniformity of the curve it would appear to consist of a single group, showing the dominant lax character only, but no definite statement as to this can be made at present. In other cases still to be described and investigated more fully, the measurements seem to indicate the existence of three groups of individuals with lax, intermediate and dense ears. The limits of each of these groups overlap, and the curves plotted from measurements of the F. 2 generation show three distinct summits.

It seems probable that if this method of analysing the F. 2 generation were capable of general application, many of the cases where it appears to be indeterminate could be explained.

Adherent and Non-adherent Paleae.

In the following cases one of the parents is naked-grained, that is, the caryopsis is set free from the paleae on thrashing, as it is in the majority of the wheats:—

H. deficiens × *violaceum.*
H. Abyssinicum × *trifurcatum.*

H. nutans × *himalayense.*
H. nigrescens × *aethiops.*

The heterozygote appears to be more or less intermediate in this respect between its parents[1]. The grains are separable from the paleae with some difficulty, and they do not rub out cleanly, as for instance, in such a typical naked barley as *H. trifurcatum.* If a handful of grain is rubbed, some grains separate completely, in some the paleae are rubbed from the back of the grain only, and others remain completely enclosed. The extent of the separation of the paleae depends to a considerable degree on the amount of weathering the ears have been exposed to.

The generation raised from the hybrids is again difficult to classify. This was also noticed by Rimpau.

A detailed examination of this pair of characters was made with *H. deficiens* and *H. violaceum.* Counting all individuals in which the paleae could be separated perfectly, or partially, by rubbing as naked-grained, 76 were placed in this group, and 25 in the group with trapped grains. Six and two rowed, coloured and colourless forms of each occurred. Sowings were made from 20 of the plants with naked grain, and all of these reproduced that feature. A similar number of trials were made with plants in which the grain was trapped, and with ten plants with partially enclosed grain, it being assumed that these latter would prove heterozygotes and the former homozygotes. It was found, however, impracticable to draw a line of demarcation between these groups, for some cultures in each were heterozygotes and some homozygotes.

An examination of the F. 2 generation of *H. nigrescens* × *H. aethiops* was made in a different manner. Instead of subjecting the grain to violent rubbing, it was stripped from the rachis and then pressed from the base upwards. Under this treatment the grain of the naked parent *H. aethiops* was readily set free from the paleae. Of 72 individuals so tested 21 were found to have truly naked grain, whilst in 51 the grain was more or less trapped. Taking the evidence as a whole, it appears that the trapped condition comes very close to being dominant over the naked, but in view of the difficulty of separating the forms in the F. 2 it is best treated, for the present, as giving an intermediate with partially naked grain.

[1] Cf. Liebscher, *ibid.*

Brittle and Tough Rachis.

In many varieties of barley the rachis is more or less brittle, but this character is only strongly marked in *H. spontaneum.* In this variety the rachis is so fragile that each group of spikelets falls as a whole as soon as ripe. The apical groups are the first to break off. The narrow grains with the stiff awn still attached fall point downwards to the ground and quickly bury themselves. This variety has been crossed with *H. hexasticofurcatum* and *H. eurylepis.* In the first case the F. 1 was a two rowed barley with trifurcate paleae, in the second, at first sight it appeared to be identical with *H. spontaneum.* As the ears ripened the rachis shattered, and the spikelets were set free as in the case of the parent. Those with trifurcate paleae were unable to bury themselves.

The F. 2 generation consisted of numerous types, as the parents differed in several features, and the brittle or tough character was distributed impartially over these. Thus brittle or tough forms with six or two rows, with hoods or awns, or with lax or dense ears were produced. The proportions were estimated at an early stage of ripeness as it was desirable to prevent the shedding of grain as far as possible, for previous experience had shown that these brittle-eared forms might readily become weeds under our conditions of cultivation. As a result of the earliness of the count some ears were not sufficiently forward enough to be classed with any certainty, and these have been neglected. In the first cross the proportions were 56 brittle to 16 with a tough rachis. In the second case the corresponding figures were 22 and 6. No further generations of these crosses have been cultivated.

In connexion with this pair of characters it should be mentioned that several of the F. 1 generations have been more brittle in the rachis than either of the parents. This was particularly the case in a cross between *H. nutans* and *H. himalayense,* the plants resulting from this mating being almost as brittle in the rachis as *H. spontaneum.* Its descendants were in a few cases slightly brittle, but it has proved impossible to sort them satisfactorily.

Awnless × Hooded Paleae.

The inheritance of the awnless character has not been investigated in sufficient detail at present, and further experiments are in progress with the object of removing this defect. The sole cross between

varieties showing these characters is that between *H. nigrosubinerme* and *H. hexasticofurcatum.* The awnless character is one of some interest, inasmuch as the character is a particularly recent one, having first come into existence in a series of hybrids raised by Rimpau from a barley with trifurcate paleae. The F. 1 generation of the cross was as awnless as the parent, and resembled it in other details to such an extent that it appeared to be possible that the cross had missed. One poor plant only was obtained which set little grain. The plants produced from this were as follows:—27 beardless, 7 hooded, and 7 awned. The beardless plants in several cases showed very small barb-like outgrowths at the ends of the paleae or on short awns of about one cm. in length. These were, as a rule, so small that a lens was necessary to distinguish them with certainty. The occurrence of the true awns was unexpected, and at first sight appears to be due to the parent itself being a heterozygote. This plant has unfortunately not been kept under observation, so in order to clear the matter up further crosses have been made.

Other minor characters.

In experiments on heredity it is inevitable that characters besides those being actually investigated should come under notice. In the case of the barleys these lesser features appear to be especially numerous, but for the most part time has been wanting to follow the inheritance of these in any detail, and attention has been directed in the main to characters of immediate importance.

Still the following short account of their inheritance will probably prove correct. Long × short grains gives long-grained forms in the F. 1 and an excess of these forms in the F. 2. This has been observed in the crosses with the long-grained *H. spontaneum.*

The broad ribbon-like awns found in such varieties as *H. japonicum*, *H. himalayense* and *parallelum* are dominant over the narrow forms occurring in the majority of the barleys. No attention has been paid to these characters in the generations raised from the hybrids. Similarly the slight awns seen on the glumes of many varieties are possibly dominant over the lack of awns found in others.

The bristly type of rachilla found in such varieties as the Goldthorpes is dominant over the smooth rachilla occurring in the Chevallier varieties. No figures have been obtained from the F. 2 generation but from data observed in the F. 3 the bristly rachilla is in excess of the smooth.

There is no evidence to show that. the Goldthorpe type of ear is necessarily associated with the bristly rachilla.

In addition to these characters the percentage of nitrogen present in the grains of F. 1 and F. 2 individuals raised from parents showing marked difference in this respect, has been followed out in some detail, as on this it is practically certain the malting value of barleys depends to a great extent. A preliminary discussion of this has already been published, and it is hoped that full details will soon be available[1].

[1] Biffen, *Journ. Brew. Inst.* Vol. XII. 1906, p. 344.

LOSSES IN MAKING AND STORING FARMYARD MANURE.

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THE objects of the investigation described in this and the following pages are two: to determine the losses in constituents of manurial value which take place in the process of making and storing farmyard manure in the ordinary course of good farming practice, and to determine the proportion of the constituents of manurial value of such purchased foods as "cakes" which actually find their way on to the land.

With these objects in view, four heifers were fed for a period of 84 days on carefully weighed and analysed diets, and at the end of the experiment the dung was weighed and analysed. From the figures so obtained, the amounts of nitrogen, phosphoric acid, and potash in the foods eaten, can be calculated, and compared with the amounts recovered in the dung.

The actual details of the experiment are as follows:

The experimental feeding began on 31 January 1906, and ended on 25 April 1906, a period of 84 days. During this time two of the animals consumed 13720 lbs. of mangels, 1176 lbs. of hay, and used up 1963 lbs. of straw as food and litter. The other two animals in the adjoining box consumed almost exactly the same amounts of mangels, hay, and straw, and in addition 672 lbs. of decorticated cotton cake.

Samples of all the foods and litter were set apart from time to time during the experiment. At the end of the time these were chaffed, pulped, or ground, as seemed best to meet the case, and small samples drawn for analysis.

The live-weight of the animals was ascertained at the beginning and end of the experiment, and from the live-weight increase, the weights of nitrogen, phosphoric acid, and potash retained in the bodies of the animals were calculated, on the assumption that these amounts would

be the same proportion of the increase in both cases, namely that given by Lawes and Gilbert for young growing animals[1]. This assumption is probably not quite accurate, since the increase in the case of the better fed animals might be expected to contain a greater proportion of fat, and consequently a smaller proportion of manurial constituents.

On 22 May 1906 the dung was sampled. At this time it was in a solid well trodden down condition, just as the animals had left it. The sampling was carried out without disturbing the dung, by cutting out a number of blocks with a hay-knife. These were well mixed, a small sample taken for analysis, and the rest replaced and trodden down. Duplicate samples were taken in this way from each box. The second sampling took place on 6 November 1906, about six months after the first. This time the samples were taken by throwing occasional forkfuls into a barrow, when the dung was being carted out of the boxes on to the land. On this occasion it was also weighed.

The weight of the dung on 22 May was calculated from the analyses, on the assumption that no loss of phosphoric acid had taken place between the two dates of sampling[2]. It was considered that this procedure would introduce fewer errors than the disturbance of the dung which would have been entailed in weighing it on the first occasion of sampling.

The analysis of the dung was carried out as follows:—2500 grams were dried by spreading out on a large enamelled iron tray which was kept on a hot plate at about 60° C. in a good draught. The drying was completed in the steam-oven. The dried dung was chaffed, and finally ground in a mill. Nitrogen was estimated in the dry-matter by Kjeldahl's method, phosphoric acid and potash in the ash of the dry matter, the latter by Laurence Smith's method. Nitrogen in the form of ammonia was estimated in the fresh dung by shaking 500 grams with 1000 c.cm. of approximately decinormal hydrochloric acid. The liquid was strained off through cloth, its total volume calculated by adding to 1000 c.cm. the volume of water contained in 500 grams of dung, as found in the dry-matter estimation, and an aliquot part distilled with magnesia into standard acid.

The boxes in which the animals were housed during the experiment were bricked up to the highest level reached by the dung. Their floors were not cemented, but were made of clay which was well rammed, and through which there could be little leakage of soluble constituents.

The following table gives the figures:

[1] *J. R. A. S. E.*, 3, VIII. 702.
[2] Cp. Dyer, *J. Agr. Sc.* I. i. 111.

	NO CAKE									CAKE FED								
	Weight, lbs.	Percentage composition				Containing by weight, lbs.				Weight, lbs.	Percentage composition				Containing by weight, lbs.			
		Dry matter	Nitrogen	Phosphoric acid	Potash	Dry matter	Nitrogen	Phosphoric acid	Potash		Dry matter	Nitrogen	Phosphoric acid	Potash	Dry matter	Nitrogen	Phosphoric acid	Potash
Mangels—Long Red	13720	13·0	0·128	0·047	0·366	1784	17·6	6·4	50·2	13720	13·0	0·128	0·047	0·366	1784	17·6	6·4	50·2
Hay—Meadow	1176	84·0	1·810	0·410	2·25	988	21·3	4·8	26·5	1176	84·0	1·810	0·410	2·25	988	21·3	4·8	26·5
Straw—mixed	1963	84·0	0·460	0·070	1·810	1649	9·0	1·4	35·5	1863	84·0	0·460	0·070	1·810	1565	8·6	1·3	33·7
Cake—Decorticated Cotton	...	...	...	...	...	...	...	...	...	672	90·0	6·37	3·18	2·40	605	42·8	21·4	16·1
Total in foods and litter..................	...	...	...	...	...	4421	47·9	12·6	112·2	...	...	...	...	...	4942	90·3	33·9	126·5
*Estimated in l.w. increase..............	152	75·4	2·54	1·72	0·22	115	3·8	2·6	0·4	326	75·4	2·54	1·72	0·22	246	8·2	5·6	0·8
Excreted by animals	...	...	...	...	...	4306	44·1	10·0	111·8	...	...	...	...	...	4706	82·1	28·3	125·7
Found in fresh dung	11333	22·85	·318	·075	·855	2590	36·0	8·5	96·9	12370	24·1	·574	·190	† —	2969	71·0	23·5	—
Loss	...	...	...	...	...	1716	8·1	1·5	14·9	...	...	...	...	...	1737	11·1	4·8	5·1
Percentage recovered in increase	...	...	...	...	...	2·6	8·0	20·6	0·4	...	...	...	...	...	5·0	9·0	16·4	0·6
,, ,, dung	...	...	...	...	...	58·6	75·2	67·5	86·4	...	...	...	...	...	60·0	78·5	69·3	—
,, loss	...	...	...	...	...	38·8	16·8	11·9	13·2	...	...	...	...	...	35·0	12·5	14·3	—
Found in dung after 6 months	8075	23·2	·383	·105	1·01	1873	30·9	8·5	81·6	8106	25·3	·576	·290	1·11	2051	46·7	23·5	90·0
Loss in storage..............................	...	...	...	...	...	717	5·1	0·0	15·3	...	...	...	...	...	918	24·3	0·0	30·6
Percentage loss during storage	...	...	...	...	...	16·2	10·6	0·0	13·6	...	...	...	...	...	18·6	26·9	0·0	24·2
,, ,, in making and storing	...	...	...	...	...	55·0	27·4	11·9	26·8	...	...	...	...	...	53·6	39·4	14·3	28·3
,, actually applied to soil ...	...	...	...	...	...	42·4	64·6	67·5	72·8	...	...	...	...	...	41·6	51·6	69·3	71·1

* Figures for growing animals. *J. R. A. S. E.* 1897, 3, VIII. 701.

† A mistake was found in this estimation, and the sample had unfortunately been destroyed before the analysis could be repeated.

The losses which occur in making farmyard manure.

The following figures abstracted from the large table give information on this point:

Dung made by	Amounts not recovered in dung or in increased live-weight per 100 parts consumed in food and litter			
	Dry matter	Nitrogen	Phosphoric acid	Potash
Animals eating roots and hay only...	38·8	16·8	11·9	13·2
Animals eating roots, hay, and cake.	35·0	12·5	14·3	—
Average loss..........................	36·9	14·6	13·1	13·4
Estimated in increased live-weight...	...	8·5	18·5	0·5
Recovered in dung	...	76·9	68·4	86·1

The duplicates agree on the whole very satisfactorily, and the figures shew that it is possible in ordinary good farming practice to recover in the fresh dung about $\frac{3}{4}$ths of the nitrogen, $\frac{2}{3}$rds of the phosphoric acid, and $\frac{7}{8}$ths of the potash contained in the food and litter consumed by the animals. Rather higher proportions would be recovered in the case of older animals, smaller amounts being retained in the live-weight increase.

The state of combination of the nitrogen in poor and rich dung.

Determinations of ammoniacal and non-ammoniacal nitrogen in each of the samples of dung were made as described above. The results are set out below.

Dung made by	Nitrogen per cent. in fresh dung			Percentage of total nitrogen	
	as ammonia	as organic compounds	Total	as ammonia	as organic compounds
Animals eating roots and hay only...	0·028	0·290	0·318	9	91
Animals eating roots, hay, and cake.	0·203	0·371	0·574	35	65

The figures shew very strikingly the effect on the composition of the dung of the use of a concentrated nitrogenous food such as decorticated cotton cake. Its nitrogen is almost entirely digestible, and consequently is excreted in the urine in the form of readily fermentable compounds which rapidly get transformed into ammonia. This leads to a great increase of ammoniacal nitrogen in the dung. Of the 42·8 lbs. of nitrogen contained in the cake consumed by the two heifers, no less than 23 lbs. can be accounted for as increased ammoniacal nitrogen in their dung. Since ammoniacal nitrogen produces a very obvious effect on the crops to which it is applied, this no doubt is the cause of the great reputation of cake-made dung.

The losses which occur during storage.

As already stated the two lots of dung were sampled twice, with an interval of about 6 months between the two dates, including the hottest months of the year. During this period of storage fermentative changes would no doubt be active, though they were minimised by the solid condition of the dung. Analyses were made on each occasion of sampling, and a comparison of the two sets of figures gives information as to the losses produced by fermentations during summer storage, with formation of ammonium carbonate which would get lost by volatilization. These figures are given below.

	Animals eating roots and hay only				Animals eating roots, hay, and cake			
	Dry matter	Nitrogen	Phosphoric acid	Potash	Dry matter	Nitrogen	Phosphoric acid	Potash
Loss per cent. in making dung	38·8	16·8	11·9	13·2	35·0	12·5	14·3	4·1
Loss per cent. in storing dung	16·2	10·6	0·0	13·6	18·6	26·9	0·0	24·2
Total loss in making and storing	55·0	27·4	11·9	26·8	53·6	39·4	14·3	28·3
Retained in live-weight increase	2·6	8·0	20·6	0·4	5·0	9·0	16·4	0·6
Percentage of manurial constituents actually applied to the land	42·4	64·6	67·5	72·8	41·4	51·6	69·3	71·1

Several points of considerable interest can be noticed in the above table. Firstly a diet enriched by cake has given a more readily fermentable dung, since the figures shew a distinctly greater loss in

dry matter from the cake dung than from that made without cake. Secondly a still greater loss has taken place in the nitrogen of the richer dung, and this is no doubt connected with the presence in it of greater proportionate amounts of ammoniacal nitrogen as shewn above. The ammoniacal nitrogen was estimated in the rotted dung. The losses of total and ammoniacal nitrogen are given in the following table.

	No Cake lbs. nitrogen	Cake lbs. nitrogen
Ammoniacal nitrogen in fresh dung	3·2	25·1
,, ,, rotted ,, ...	1·9	10·0
Loss of ammoniacal nitrogen during storage..................	1·3	15·1
,, ,, ,, as percentage of total loss...	25	62

The dung of the cake-fed animals contains eight times as much ammoniacal nitrogen as the poorer dung, and about two-thirds of this is lost during storage. This great loss of ammonia accounts for 62 per cent. of the total loss during storage in the richer dung, while in the poorer dung, of the smaller amount of ammonia present only about one-third is lost which accounts for only 25 per cent. of the total loss from this lot of dung. It will be remembered that the assumption was made that no phosphoric acid was lost in storage. There is a certain loss of potash, during storage, and the proportion of the total potash consumed by the animals in food and litter which finally reached the land was only about three-quarters, instead of the whole as estimated by Voelcker and Hall. The amount of phosphoric acid which was found in the rotted dung also falls short of Voelcker and Hall's estimated three-quarters by 6 or 7 per cent. The figures for nitrogen come rather over their limit of 50 per cent. though the amount in the rotted dung from the cake-fed animals cuts it rather fine.

The manurial value of cotton cake.

Since the two pairs of animals consumed practically equal amounts of hay, straw and roots, and since the dung of each pair was similarly treated throughout the experiment, it is possible, taking the no-cake dung as a base-line, to calculate from the figures already given the amounts of the manurial constituents of the cake which were recovered in the dung. The figures for this are given below.

	Dry matter	Nitrogen	Phosph. Acid	Potash
Fresh manure:	lbs.	lbs.	lbs.	lbs.
Animals eating roots, hay, and cake	2969	71·0	23·5	—
Animals eating roots and hay only	2590	36·0	8·5	96·9
Constituents of cake recovered in dung	379	35·0	15·0	—
Constituents contained in cake eaten	605	42·8	21·4	16·1
Percentage of manurial constituents of cake recovered in fresh dung	63	82	70	—
Rotted manure:				
Animals eating roots, hay, and cake	2051	46·7	23·5	90·0
Animals eating roots and hay only	1873	30·9	8·5	81·6
Constituents of cake recovered in dung	178	15·8	15·0	8·4
Constituents contained in cake eaten	605	42·8	21·4	16·1
Percentage of manurial constituents of cake which actually reached the land	29	37	70	52

The highly fermentable nature of the cake residue is very evident. While 63 per cent. of the dry-matter of the cake was recovered in the fresh dung, less than half that proportion remained in the dung after 6 months' storage. This proneness to fermentation causes great losses of nitrogen, for the fresh dung contains 82 per cent. of the nitrogen of the cake, as against 37 per cent. in the dung when ready for application to the land. This point seems to be one of considerable practical importance for the following reasons.

When a tenant leaves a farm he is compensated by valuation, not for the total manurial constituents contained in the dung he leaves behind in the yards and buildings and in the soil, but for those constituents only which were presumably derived from the foods, such as cakes, which he had purchased during the last years of his tenancy. In the case under consideration compensation would be paid on the manurial residue of 672 lbs. of decorticated cotton cake. If the compensation due on this were valued on the basis of Voelcker and Hall's estimates, payment would be due on half the nitrogen, three-quarters of the phosphoric acid, and the whole of the potash. But these estimates appear to have been based on experiments in which the measurements made were the proportions of the manurial constituents of the whole diet which were recovered in the dung. In other words compensation is assessed on the assumption that the losses in making and storing dung are practically the same for all the constituents of a diet.

The experiment which is described in the present communication shews clearly that this is not the case, and theoretical considerations seem to support this contention. Thus taking Wolff's figures for the digestibility of the nitrogen of the foods used in the experiment, it appears that of the 48 lbs. of nitrogen consumed as food and litter by the animals receiving no cake, 30 lbs. only would be digested. Subtracting from this the 4 lbs. retained in the form of increased live-weight, it follows that these animals would have excreted in their urine about 26 lbs. of nitrogen. The balance of 18 lbs. would exist in insoluble compounds in the solid excreta, or in the litter. In the same way it is arrived at that the cake-fed animals would excrete about 56 lbs. of soluble nitrogen in their urine and about 26 lbs. in their solid excreta and litter. The richer dung would therefore contain more than twice as much soluble and consequently readily fermentable nitrogen as the poorer, and would be proportionately more liable to suffer loss by fermentation, volatilization, and drainage. If the dung were stored for any length of time before being put on the land, the richer the dung the more rapidly might it be expected to lose nitrogen, and consequently, although more than half the total nitrogen of the food and litter might, with reasonably good management, reach the land, it by no means follows that a quantity of dung, made with the addition of say 1 ton of cake, containing 100 lbs. of nitrogen, would contain 50 lbs. more nitrogen than the dung made from the same amounts of home-grown foods without the addition of the cake. Yet it would be on this 50 lbs. of nitrogen that Voelcker and Hall would estimate for compensation.

In the experiment under discussion, out of 100 lbs. of nitrogen in the cake, only 37 lbs. could be traced in the dung at the time when it was applied to the land. Of this 37 lbs., a considerable proportion was found to be in the form of ammonia, and a still further loss might therefore easily take place if the dung were allowed to lie for any length of time on the surface of the land in dry weather. The actual proportion of the nitrogen of the cake which was recovered in the dung in the experiment varied from 82 per cent. in the fresh dung to 37 per cent. in the rotted dung, and probably even less than 37 per cent. would find its way into the land. The dung was however stored for a longer period, and at a hotter time of year, than is usually the case in farming practice, and the average proportion recovered is therefore probably between the limits found in the experiment for fresh and rotted dung, i.e. between 82 and 37 per cent., and this agrees very well with Voelcker and Hall's estimate of 50 per cent. The point should

not however be lost sight of that the loss in storage and in application to the land falls chiefly on the ammoniacal nitrogen of the cake-made dung, and is so great that the proportion of the nitrogen of the cake which actually finds its way on to the land may, without any flagrant mismanagement, very easily fall below 50 per cent.

Summary.

Two pairs of young heifers were fed on a weighed and analysed diet, and their dung was sampled and analysed both in the fresh and in the rotted states.

It was found that the fresh dung contained about $\frac{3}{4}$ths of the nitrogen, $\frac{2}{3}$rds of the phosphoric acid, and $\frac{7}{8}$ths of the potash consumed by the animals in food and litter.

The dung made by the cake-fed animals was found to be more readily fermentable, and consequently more liable to loss during storage, than that made by the animals fed on roots and hay only.

The loss was found to fall chiefly on the ammoniacal nitrogen in which the cake-made dung is comparatively very rich.

Taking as a base-line the amounts of nitrogen and phosphoric acid in the dung of the animals fed on roots and hay only, it was found that the fresh dung of the cake-fed animals contained 82 per cent. of the nitrogen, and 70 per cent. of the phosphoric acid, of the cake they had consumed.

So great however was the loss of ammoniacal nitrogen from the cake-made dung, that after 6 months' storage under cover in the solid undisturbed state in which it was left in the boxes by the animals, only 37 per cent. of the nitrogen of the cake still remained in the rotted dung.

Dung is not usually kept so long as this, nor through such a hot time of the year, so that the average loss will probably be less than that found in the experiment, and $\frac{1}{2}$ the nitrogen of purchased foods may very well be the average amount recovered in the dung.

The experiment shews however that, without any very flagrant mismanagement, the proportion recovered may fall considerably below $\frac{1}{2}$, especially if the dung suffers further loss while lying on the surface of the land in dry weather.

NOTE ON MENDELIAN HEREDITY IN COTTON.

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EXPERIMENTS carried out at Ghizeh during 1905 and 1906 shew that the cotton plant follows Mendel's laws of gametic segregation in certain of its characters.

The initial stages of the work were devoted to gathering evidence as to the gametic constitution of the field crop as grown in Egypt. It was found that the individuals of any variety varied extensively except in regard to lint colour. In fact it is doubtful whether any pure types are in cultivation in the country.

An analysis of the offspring of single plants has shown that cross-fertilisation takes place to a certain extent under field conditions and the accumulated effect of this has been to convert the crop into a mass of hybrids. A weed cotton is also present in the crop. This is readily removable by selecting but it would be difficult to eradicate the splitting forms arising from natural crosses with the cultivated varieties.

F. 2 generations of a number of natural crosses have been analysed in respect of their seed characters with results which show that long lint is completely dominant over short. In crosses between distinct types of cottons such as Uplands and Egyptians the lint of the first picked bolls of the F. 1 plants is greater than that of the dominant parent, but in the bolls which ripen later it has the same length as that parent. A similar fluctuation of lint length occurs in cottons grown in a favourable environment, longer lint being found in the bolls of the first picking, whilst in the later various lengths may be found on different seeds even from the same boll. The same cottons grown under less favourable conditions produce lint of a uniform length. Between these extremes the difference may be as much as 12 %.

The inheritance of the colour of the flowers appears to be more complex, and the details of this have still to be investigated. From the evidence obtained at present there is a great probability that time of ripening is a Mendelian character, and if this proves to be the case it should be practicable to check the ravages due to the attacks of the boll-worm (*Earias Insulana*) by raising early maturing varieties.

The breeding of pure types suitable to the needs of the manufacturer and the cultivator will possibly prove a little difficult, owing to the fact that many of the characters of economic importance are dominant.

REVIEWS.

Mendelism. R. C. Punnett. [Cambridge: Macmillan and Bowes.] The appearance of a second edition of this admirable little primer is a sign that the biological principles enunciated by the distinguished Abbot of Brünn are engaging an increasing amount of scientific attention. That they are not yet formally applied by the practical breeder may be granted, but that progress has, in the past, been unwittingly effected along Mendel's lines cannot be denied. If Mendel's induction does not furnish the key to all the problems that confront the farmer and gardener, that is simply because the intricacy of the wards of the locks of some of the inner compartments has not yet been fully mastered. But we have now been admitted to the vestibule of knowledge, and it is only a question of time when all the doors will yield.

So far experimentation has been largely confined to animals and plants of relatively small economic importance. Peas and poultry are more easily controlled than cattle and cereals, and so they have received more attention. Biffen's work on wheat is a notable exception, and now we want to see one of the great divisions of farm animals similarly taken in hand. A bigger loaf should have for its complement a corresponding increase in beef and mutton, and that the latter can be secured by the same methods as the former admits of no reasonable doubt. Mr Punnett's book, with its helpful illustrations, may be confidently recommended alike to students and breeders as a clear exposition of the elements of a none too simple subject.

Recent Progress in the Study of Variation, Heredity and Evolution. R. H. Lock, M.A. [John Murray, 7*s.* 6*d.* net.] Among recent scientific discoveries probably none are of such direct importance to the practical breeder of plants and animals as those which have been made in the field of Variation and Heredity. Pure science is often regarded as dealing with matters which are of no practical importance, but in the work under review a description is given of work which was not undertaken with the direct object of benefiting agriculture, yet

which is of enormous practical value. At the present time the methods used in selection for breeding, and in crossing different breeds, are chiefly empirical, and those engaged in such work do not trouble themselves much with the principles involved. But the recent work here described has shewn that the principles are in themselves simple, and that by understanding and following them the work of the breeder is not only made much easier, but also much more certain of success. No one can read the pages dealing with the results already obtained with maize, wheat and barley, without being convinced that they are of the utmost importance to agriculture.

The book is intended chiefly for the general reader interested in biological science, and all parts of it will not appeal equally to those whose chief interest is agriculture. The first three chapters are devoted to the problems of the Origin of Species, Evolution, and Natural Selection, and give a summary of our knowledge on these subjects before the more recent discoveries were made. The fourth chapter deals with the statistical study of variation, and although it may be difficult reading for those who have no previous acquaintance with the subject, yet it contains conclusions of great importance to the breeder of plants and animals. For example, on pp. 107, 108 the work of Prof. K. Pearson is quoted, shewing that it is impossible to establish a permanent breed simply by selection of minute variations, for if the selection is discontinued the race will tend to degenerate. More important is the conclusion of Prof. Johannsen (pp. 108—112), that within what is considered a single race, there are numerous sub-races each of which can be isolated and cultivated separately, and that the only safe and rapid means of improvement by selection is to isolate the best race by breeding *individual plants* (in this case barley and kidney beans), and choose the plant which gives the best offspring from which to obtain seed.

The following chapters deal with the occurrence of large variations (sports, mutations), and with the manner in which they are inherited. These chapters are the most important in the book, and are full of valuable information. Chapter v. shews how the various races of plants and animals, each of which is distinct from the other races of the same species, have arisen in all cases where we know of their origin by comparatively large definite variations, which have been preserved, propagated and improved by selection till a race is established. Chapter vi. is chiefly historical, shewing the confused state of our knowledge of hybridization before the new work gave the clue.

The central idea of the book is contained in Chapters VII. and VIII., and it is these chapters which are of primary importance to agriculture. They deal with the question of crossing races possessing different characters, and with the way these characters appear in the offspring of such a cross. It is impossible in a short review to give an idea of Mendel's Law which is here described, but an outline may be attempted. We will take an example from Mr Lock's own investigations, described by him on pp. 166—172. In maize the grains may be yellow or white. If a plant belonging to the race with white corn is fertilized by pollen from the yellow-grained variety, all the grains in the cob (the first-crossed generation) are yellow. The yellow colour is thus said to be *dominant.* If now such yellow hybrid grains are sown and the resulting plants are self-fertilized, on their cobs $\frac{3}{4}$ (75 per cent.) of the grains are yellow, and $\frac{1}{4}$ (25 per cent.) are white. When these grains are sown it is found that the white breed true; they are absolutely pure and uninfluenced by their crossed ancestry. Of the yellow grains, $\frac{1}{3}$ (i.e. $\frac{1}{4}$ of all the grains on the cob) are also pure and breed true, and the remainder are dominant hybrids which will yield yellow and white in the same proportions as before. Here then we have a fact not generally appreciated by breeders, that *absolutely pure* individuals may be bred from crossed parents. But another fact of greater importance follows (see p. 174 ff.). If the original parents from which the first cross is made differ in two pairs of characters, e.g. one is yellow and contains starch, the other white containing sugar, then in the first cross all the grains will be yellow with starch, because both these characters are dominant, but when self-fertilized they will yield not only yellow starchy and white sugary, but also white starchy and yellow sugary grains, and a definite proportion of the plants so obtained will breed perfectly true. Here then by crossing we have obtained two new varieties, and by examining the offspring of the *separate plants* we can tell which are pure, and so obtain in two generations a pure race combining the characters of both parent races. The practical importance of this is shewn by the description on pp. 215—221 of the work of Mr Biffen on Wheat, which shews how it is possible to unite such valuable characters as strength with the power of yielding large crops in the English climate, or of combining other important qualities with non-liability to rust. Cases are also given of almost equally interesting discoveries in animals, of which the Andalusian fowl (p. 181) is an example.

A short summary of this kind cannot sufficiently impress the reader with the vast importance to anyone who wishes to undertake the im-

provement of any race of plant or animal of a knowledge of the simple principles involved. The confusion consequent on crossing is shewn to result from the want of discrimination of *separate* characters; when each character is taken alone it obeys simple laws. The fact of the dominance of certain characters is also of great importance, for if a character is completely dominant, the purity of the individual exhibiting it can only be tested by breeding it separately. As an example of the confusion which arises from want of knowledge on this point, we quote the following sentence from a recent paper on the selection of seeds of the cotton-plant. "It is highly important in practice to select more than one excellent plant, as it not infrequently happens that a very fine plant is found having poor transmitting power...." This really means that before selecting a plant for seed one must test its purity in the character required (if that character be 'dominant'), lest the plant turn out to be a hybrid.

The essence of the matter is that single characters must be treated separately, and that the composition of individual plants must be tested, not by their ancestry, but by their progeny, for if this is done the process of selection is enormously simplified.

Mr Lock's book should be read by all interested in these matters; it is interesting throughout, generally clearly written, and has a good index and a glossary of technical terms for those who have no great acquaintance with the subject. And it has the further advantage of giving a great deal of information in a very small space.